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VOLUME 32 SEPTEMBER, 1958 NUMBER 5

STRATIGRAPHIC SIGNIFICANCE OF MISSISSIPPIAN ENDOTHYROID FORAMINIFERA IN CENTRAL UTAH

ROLAND BERT WOODLAND
Brigham Young University

ABSTRACT—Study of thin-sections from samples of the Mississippian sequence in central Utah has yielded biostratigraphic data on the occurrence of endothyroid foraminifera. Distribution of these foraminifera in the Provo Rock Canyon section suggests four faunal zones. They are from the bottom up: *Granuliferella* zone and *Plectogyra tumula* subzone, *Endothyra symmetrica* zone, and *Plectogyra kleina* zone.

New species of the genera *Granuliferella, Plectogyra,* and *Endothyra* are as follows: *G. asperata, G.? granulella, P. gibbosa, P. turgida, P. bullata, P. kleina, E.? lanceolata,* and *E. hamula.*

Comparative phylogeny can be used to correlate upper Mississippian time equivalents between central Utah and Mississippi Valley. Lower Mississippian forms of the two areas are dissimilar and correlation is uncertain.

A vagrant benthonic habit of endothyroids during life is indicated by limited lithologic association with unabraded echinoderm stem segments, irregularity of form, and granular wall of individuals. Flood occurrence is attributed to biological and ecological agents which periodically killed and preserved sensitive populations en massé. Negligible influence of sedimentary sorting on flood abundance is shown by association with unbroken and unabraded macrofossils and echinoderm stem segments. Meaning of euhedra and subhedra of calcite in encrinal rocks is not known with certainty but may have grown contemporaneous with deposition. Endothyroid sensitivity to environment is indicated by their diminished abundance or complete absence in rocks of non-calcareous composition and non-encrinitic texture.

INTRODUCTION

Previous work.—The first significant contribution to the stratigraphic paleontology of the endothyroids was by E. J. Zeller (1950). This work was not a systematic study of the endothyroids but showed conclusively that they can be used as stratigraphic markers. Phylogeny was diagrammatically illustrated and obvious specific variation of populations demonstrated stratigraphic value of Mississippi Valley endothyroids. Seven years later (1957) E. J. Zeller published systematic descriptions and faunal zonation of Cordilleran endothyroids. Other workers Plummer (1930), Henbest (1931), Scott, Zeller, & Zeller (1947), D. E. Zeller (1953), and St. Jean (1957) have published stratigraphic and taxonomic studies of the endothyroids.

The genus *Endothyra* was first recognized by Brown (1843). Three years later Phillips (1846) published a description of *Endothyra* but his figured specimen of the type species *Endothyra bowmani* differs from Brown's. Brown clearly gave authorship of the genus to Phillips, not to himself. Some confusion has arisen as to who the original author is

and consequently, what the generic characters should be. Following the rules of zoologic nomenclature Scott, Zeller, and Zeller (1947) interpreted Phillips the first author of the genus. E. J. Zeller (1950), one of the above three authors, reversed his decision and considered Brown the original author. In the same paper Zeller recognized earlier authors had placed forms with twisted coiling in *Endothyra* which he felt did not belong in the genus. A new genus *Plectogyra* was erected to include endothyroids with a twisted coil. *Endothyra* was interpreted to have a planispiral coil.

St. Jean, Jr. (1957, p. 24–26) attacked the validity of *Plectogyra* E. J. Zeller, and synonymized *Plectogyra* with *Endothyra*. For the reader's convenience St. Jean, Jr. (1957, pl. 1, fig. 3) reproduced Phillips' figure of the type specimen of *Endothyra*. This paper recognized Phillips as author of *Endothyra* but interpreted the type specimen as having an asymmetrical coil. The writer does not share St. Jean's enthusiasm for supressing *Plectogyra*. Distortion or asymmetry of the coil is not detectable in Phillips' figure of the genotype *Endothyra bowmani*. Perhaps St. Jean's asymmetrical coil does not have the same definition as Zeller's distorted or plectogyroid coil. *Plectogyra* is used in this work in the same sense Zeller defined the genus.

In a Russian paper, Chernysheva (1940) described a new Mississippian foraminifer *Paraendothyra* bearing the generic characters of *Plectogyra*. He also figured specimens with plectogyroid coiling which he called *Endothyra* and *Brunsia*?. Observation of Chernysheva's plates suggests *Paraendothyra* was erected on character other than coiling. If *Paraendothyra* was established on coiling of the shell, it has precedence over *Plectogyra*. A complete translation of Chernysheva's description of *Paraendothyra* will give a better basis for determining the reason his new genus was erected.

Both St. Jean (1957) and Chernysheva (1940) came into the writer's possession after the manuscript for this paper was prepared. Examination of Brown's and Phillip's original work and opportunity for thorough study of Chernysheva's and St. Jean's papers may change the writer's views on the validity of *Plectogyra*.

Purpose of present work.—Doctors Harold J. Bissell and J. Keith Rigby jointly suggested this study. The principle objective was to systematically describe endothyroids in central Utah for an attempt to separate the Mississippian sequence into faunal zones. Approximately 900 thin sections were prepared before enough data were collected to satisfy the principle objective.

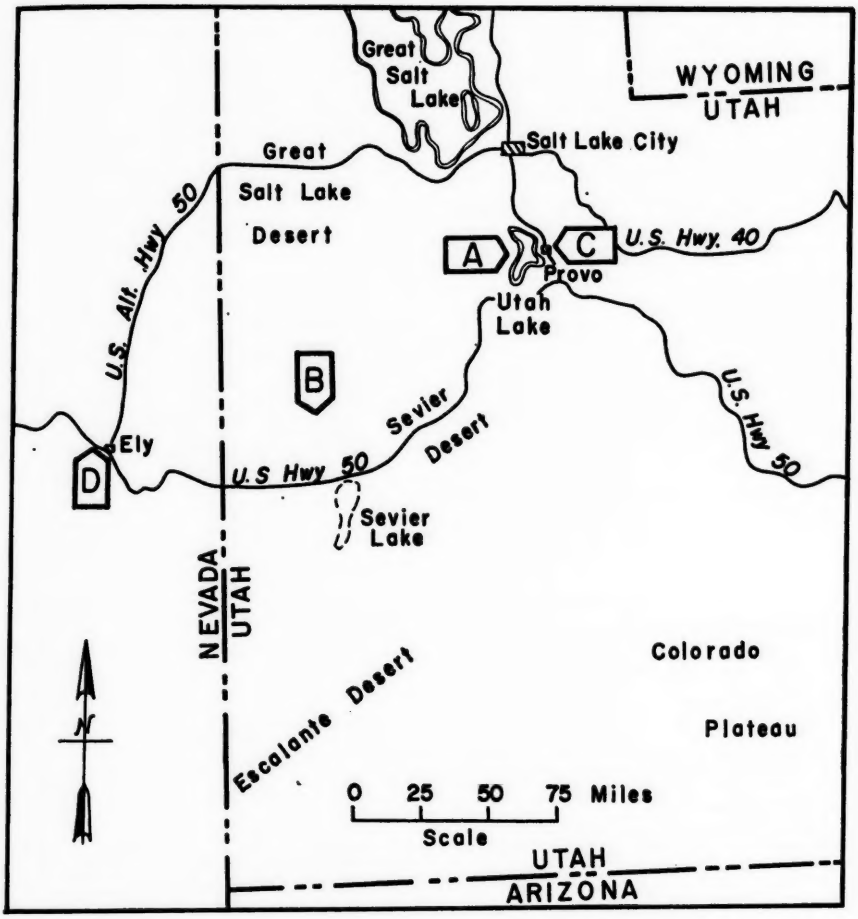
Phylogentic development of central Utah endothyroids became a secondary objective and is used to attempt inter-basin correlation with Mississippi Valley. Observation of thin-sections showed flood occurrence and abundance distribution data were feasible and are used for ecological interpretations.

The systematic descriptions presented here are not intended to completely describe endothyroid shell morphology. Rather, they present enough detail to permit speciation for the purpose of faunal zonation.

Three or four genera and an estimated twenty to thirty species of foraminifera were encountered in thin-sections which are not described or illustrated. Most of these are rare occurrences. Additional thin-sections will probably expand the number of describable foraminiferal genera and species of the Mississippian in the Cordilleran basin.

Field procedures.—Systematic abundance and zonation data are recorded from only the Provo Rock Canyon section. Stratigraphic measurements were taken simultaneously with samples and stratigraphic distance from the base of each formation numbered in yellow paint on the canyon wall at thirty to forty foot intervals. Samples were given corresponding numbers. Also, a yellow "X" was marked at each sample locality between the yellow stratigraphic markers.

Oolites and encrinal beds usually contain endothyroids in large variety and abundance. These strata were sampled at two to three foot intervals. Endothyroids are less abundant or may be completely absent in rocks with non-calcareous composition and non-encrinitic texture. Samples in these strata were taken every ten to fifteen feet to check occurrence. Each sampled bed in the Provo Rock Canyon section can be found by using as guides the locality descriptions in



TEXT-FIG. 1—Index map of fossil collecting localities.

this work and the writer's field notes on file with the Department of Geology, Brigham Young University.

Samples from Cedar Valley Hills and Conger Mountain sections were taken at random intervals by the writer in encrinal beds. Stratigraphic positions were estimated and recorded.

The Ely, Nevada, section was measured and sampled by Doctor Harold J. Bissell. Only chips showing abundant echinoderm fragments were thin-sectioned from these samples.

Laboratory procedures.—Endothyroids are not detectable in hand samples even under high magnification. Disaggregation, acetate peels, and thin-sections were all tried in preparation of endothyroids for study. Attempts at disaggregation of friable limestone samples failed to release any individuals. Acetate peels do not show zoologic characters in identifiable detail. Thin-sections are the only useful method for studying endothyroids enclosed in limestone.

Experimental orientations of some of the samples showed the greatest number of sagittal and horizontal axial sections were obtained in thin-sections cut parallel to bedding. Endothyroids usually came to rest after death with one of their flat sides on the bedding plane. Since identifications are positive only in sections cut parallel to the plane of coiling, all samples were cut parallel to bedding.

SECTIONS SAMPLED

Section A—Cedar Valley Hills, Utah County, Utah.—Collection was started in the Gardner limestone at the base of the hill on the first significant spur north of Cedar Valley Rock Canyon. The point is located on the Saratoga Springs quadrangle in the N½ SE¼ NE¼ NW¼ sec. 32, T. 6 S., R. 1 W. Collection from this point commenced up the spur to the top of the hill at the Humbug-Great Blue formational contact. This point is located at the SE cor. N½ SE¼ SE¼ sec. 29, T. 6 S., R. 1 W. An offset to the south 1900 feet at the base of the Great Blue limestone was made to collect the thickest sequence of Great Blue rocks in the area. The offset location is at the center NW¼ SE¼ NE¼ sec. 32, T. 6 S., R. 1 W. Great Blue limestone samples were taken in a northeasterly traverse to the top of the hill at center NW¼ NW¼ NW¼ sec. 33, T. 6 S., R. 1 W.

Section B—Conger Mountain, Millard County, Utah.—The Joana limestone on the east flank of the Conger Anticline, located on the Fish Springs quadrangle, was sampled by the writer on a cliff 0.6 miles east of 113° 45′ meridian, 4.7 miles south of 39° 15′ parallel, and 2.8 miles southwest from the peak of Conger Mountain.

Section C—Provo Rock Canyon, Utah County, Utah.—The Provo Rock Canyon section is located in the southwest corner of the Bridal Veil Falls quadrangle. Sampling began at the Mississippian-Cambrian unconformity approximately 0.8 miles above the first fork in the road at the mouth of the canyon and approximately thirty feet west of the first wooden bridge. The unconformity in the bottom of the canyon is located in S½ SW¼ NE¼ SW¼ sec. 28, T. 6 S., R. 3.E. From this point samples were collected upstream, in nearly vertical strata. Encrinal rocks weather rapidly to form topographic lows and some of the vertical strata are covered at the bottom of the canyon. It was necessary to collect from these beds in cliffs on the north wall of the canyon above talus slopes.

Sampling progressed upstream in this manner to the First Left Fork of Rock Canyon, then northeasterly up the face of the hill separating First Left Fork and Second Left Fork to a point on top of the hill 800 feet southeast of the intersection of sections 21,22,28, and 27, T. 6 S., R. 3.E.

Section D—Ely District. White Pine County, Nevada.—The Joana limestone was measured and sampled by Doctor Harold J. Bissell northeast of the type area in a section one mile northwest of the junction of Ruth road with U. S. Highway 50, five miles northwest of Ely, Nevada.

DEFINITION OF TERMS AND ENDOTHYROID SHELL MORPHOLOGY

Acanthus (Latin: "thorn") shall be used to indicate a secondary deposit sharply

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EXPLANATION OF PLATE 99

All figures ×50

FIGS. *1,4,6—Plectogyra kleina*, n. sp. Horizontal axial sections; *1.* loc. BYU10980-LA, specimen BYU147F; *4*, the holotype, loc. BYU10988-341, specimen BYU144HT; *6* loc. BYU10980L, specimen BYU115F.

2,3—Granuliferella sp. Horizontal axial sections; *2*, loc. BYU10992-322C, specimen BYU114F-A; *3*, loc. BYU10992-322C, specimen BYU148F-E.

5—Plectogyra sp. Horizontal axial section, loc. BYU10980-L, specimen BYU140F-B.

7,8,12,14—Granuliferella granulosa E. J. Zeller. Horizontal axial sections; *7*, loc. BYU10992-551A, specimen BYU125F-A; *8*, loc. BYU10992-266, specimen BYU101F-B; *12*, loc. BYU10992-551, specimen BYU152F-D; *14*, loc. BYU10992-551, specimen BYU153F-F.

9,10,11,13,18,19—Granuliferella? granulella, n. sp. *9,10,18*, Horizontal axial sections; *9*, the holotype, loc. BYU10992-554B, specimen BYU126HT-B; *10*, loc. BYU10992-551D, specimen BYU151F-A, *18*, elongated and flattened by crushing, loc. BYU10992-551, specimenBYU 156F-B; 11, oblique axial section, loc. BYU10992-381B, specimen BYU127F-C; *13*, vertical axial section, loc; BYU10992-551, specimen BYU122F-A.

15–17—Granuliferella asperata, n. sp. Horizontal axial sections; *15*, loc. BYU10992-306, specimen BYU105F; *16*, line drawing of specimen not showing aperture, loc BYU10992-306A, specimen BYU106F; *17*, the holotype, loc. BYU10992-298, specimen BYU104HT.

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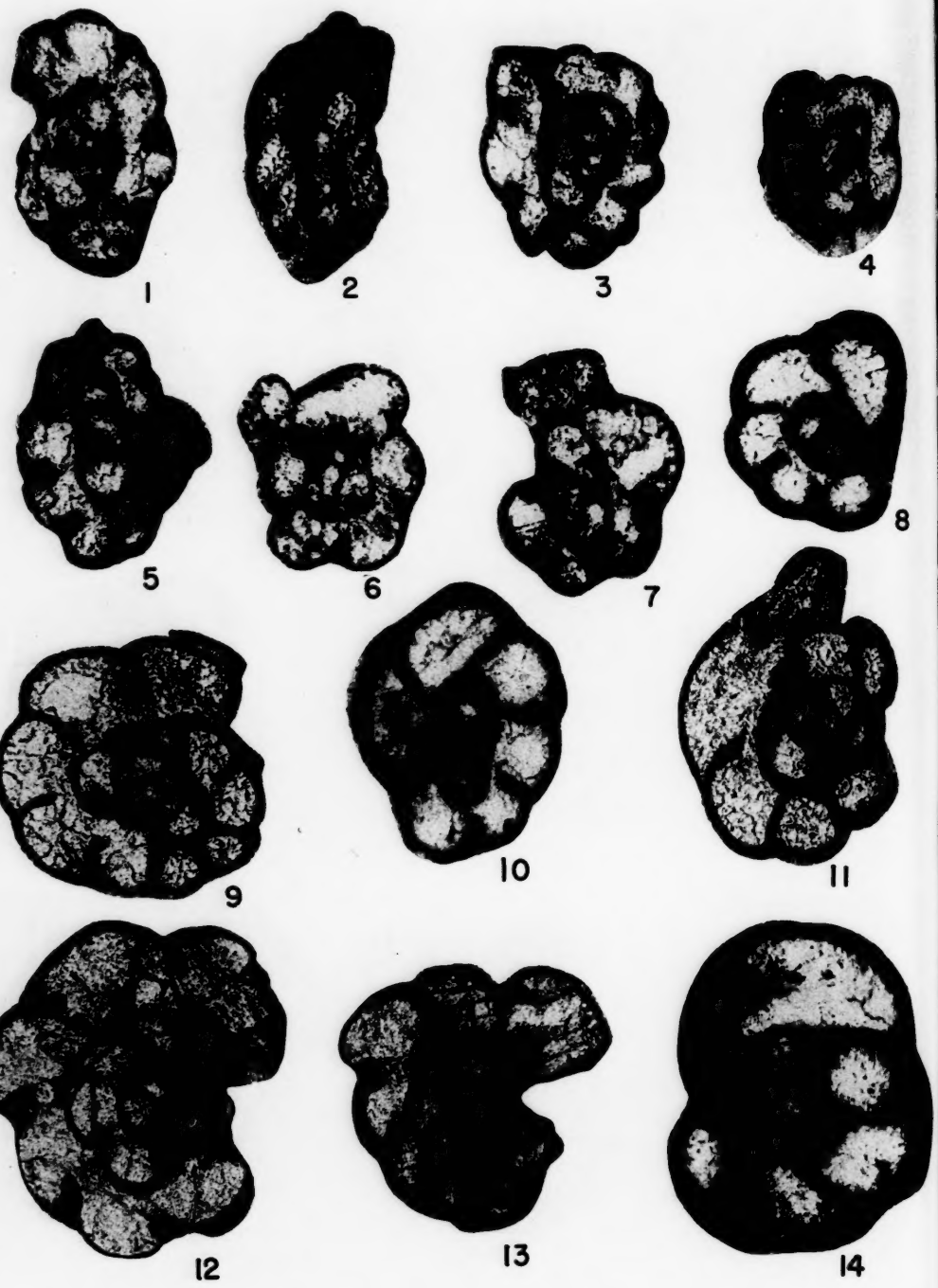
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pointed but not curved toward the anterior.

Encrinite is an echinoderm coquina with calcareous matrix and cement.

Endothyrid shall be used in reference to all species of the planispirally coiled genus *Endothyra*.

Endothyroid shall be used in reference to all foraminifers in the family Endothyridae.

Granuliferellid shall be used in reference to all members of the plectogyroid coiled genus *Granuliferella*.

Hamulus (Latin: "hook") shall be used to designate a hook-shaped deposit in which the point of the hook is pointed toward the anterior.

Plectogyrid shall be used in reference to all species of the plectogyroid coiled genus *Plectogyra*.

Plectogyroid shall be used to indicate endothyroids with a plectogyroid spiral, formerly called the "endothyroid spiral."

Plectogyroid spiral is a three dimensional figure produced by a point moving in a plane so as to generate a logarithmic spiral while the plane is simultaneously rotated about an axis passing through the center of the spiral.

Tumulus (Latin: "a little hill") shall be used to indicate that type of secondary deposit which appears in cross-section as a more or less symmetrical node with a rounded summit.

The three terms dealing with secondary deposits were originally defined by Zeller (1957 p. 693) and are used in the same sense in this work. The plectogyroid spiral was suggested by Zeller (1950, p. 3) to be used in preference to endothyroid spiral since the character is limited to the genus *Plectogyra*. *Plectogyra tumula* (text-fig. 3—11) shows well-developed tumuli. *Endothyra* sp. (Text-fig. 3—19) shows an acanthus very slightly curved toward the anterior. A well-developed hamulus is seen in the last chamber of *Endothyra hamula* (text-fig. 3—18). The definition of plectogyroid spiral is taken from and identical to the Scott, Zeller, and Zeller (1947, p. 558) definition of the endothyroid spiral.

Encrinite has the same meaning as the Pettijohn (1949, page 301) definition. The remaining terms are convenient in referring to various endothyroid forms and have loose biologic meaning. Some of these terms have been previously used but none have been defined.

The wall structure of endothyroid foraminifera is frequently poorly preserved and consequently unusable in these specimens for classification. Members of the genus *Plectogyra* with imperfectly preserved walls are especially difficult to differentiate from the thin-walled granuliferellids. The principal distinguishing feature is the separation of the plectogyrid wall into layers. This layering is not distinguishable in poorly-preserved individuals. In such cases identification of the genus is dependent upon other morphological characteristics of coiling, dimensions, and relative size of chambers. Granuliferellids are generally small, have two or less volutions, show large angular

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EXPLANATION OF PLATE 100

All figures ×50

FIG. *1*—*Plectogyra* sp. Horizontal axial section, loc. BYU10992-322C, specimen BYU116F-C.

2–5—*Plectogyra? gibbosa*, n. sp. Horizontal axial sections; *2*, loc. BYU10992-322D, specimen BYU117F-A; *3*, the holotype, loc BYU10992-322C, specimen BYU173HT-B; *4*, loc. BYU10992-322D, specimen BYU118F-B; *5*, loc. BYU10992-322B, specimen BYU112F-A.

6,7—*Granuliferella tumida* E. J. Zeller. Horizontal axial sections; *6*, loc. BYU10992-322, specimen BYU109F-C; *7*, loc. BYU10992-322A, specimen BYU111F.

8,10,14—*Plectogyra turgida*, n. sp. *8,10*, horizontal axial sections; *8*, loc. BYU10983-B, specimen BYU157F; *10*, loc. BYU10983-E, specimen BYU158F; *14*, oblique axial section, loc. BYU10983, specimen BYU159F.

9,11—*Plectogyra tantala* D. E. Zeller. Horizontal axial sections; *9*, loc. BYU10990-278, specimen BYU135F-A; *11*, loc. BYU10990-278A, specimen BYU136F.

12,13—*Plectogyra bullata*, n. sp. Horizontal axial sections; *12*, the holotype, loc. BYU10992-322B, specimen BYU113HT-B; *13*, loc. BYU10992-322E, specimen BYU120F.

distortion of the spiral, and have large chambers in comparison to size of individuals. *Granuliferella tumida* (text-fig. 3—4) shows the generalized characteristics of thin-walled granuliferellids. Generic differentiation of the plectogyrids and granuliferellids not based on wall structure is risky and caution should be used. Plate 103, figure 10, is greatly enlarged photograph of *Granuliferella? granulella* representing a typical thick, single layered, granular, granuliferellid wall.

The plectogyrid wall is not differentiated from the endothyrid wall. The walls of *Endothyra* and *Plectogyra* in well preserved individuals are separated into three primary layers, an inner dark layer, the tectorium, a relatively thick, clear intermediate layer, the diaphanotheca; and an outer thin, dark layer, the tectum. A fourth layer, which may be missing, can, if present, be referred to as the outer tectorium. The fourth layer is responsible for the need of terms dealing with secondary deposits. A sketch of *Plectogyra tantala* (pl. 103, fig. 9) is the same specimen as shown in plate 103, figure 11 and aids the reader in recognizing individual wall layers.

Generic differentiation of *Endothyra* and *Plectogyra* is based on coiling of the shell. An individual with the slightest degree of angular distortion is placed in the genus *Plectogyra*. Planispirally coiled endothyroids are classed with the genus *Endothyra*. Planispiral forms are represented on text-fig. 3—3, 12, 15, 17, 18, and 19. Text-fig. 3—21 is a plectogyrid with small angular distortion; text-fig. 3—20 shows large angular distortion.

The following wall thickness dimensions standardize the relative qualitative values of thin, medium, and thick.

Qualitative Value	*Quantitative Value*	*Representative Species*
Thin	0.015 mm.	*Granuliferella tumida*
Medium	0.025 mm.	*Endothyra symmetrica*
Thick	0.040 mm.	*Granuliferella granulosa*

ACKNOWLEDGMENTS

The writer is grateful to Drs. J. Keith Rigby and Harold J. Bissell who jointly suggested research in endothyroid paleontology. Dr. Rigby acted as thesis advisor and offered suggestions which aided in research and preparation of the manuscript. Drs. Harold J. Bissell, Lehi F. Hintze, Kenneth C. Bullock, George H. Hansen and Messrs. Jess R. Bushman and Willis H. Brimhall have read the manuscript and made helpful criticisms. The writer's brother, Steven, assisted field and laboratory work. Last but by no means least, the writer expresses gratitude to his wife, Carla, who cheerfully bore the secretarial responsibility of this work.

SYSTEMATIC DESCRIPTIONS

Genus GRANULIFERELLA E. J. Zeller, 1957

Granuliferella E. J. ZELLER, 1957, p. 694.

Genotype.—*Granuliferella granulosa* E. J. Zeller.

Description.—Shell discoidal, involute, small to intermediate in size, more umbilicate on one side than the other; chambers large in proportion to size of shell, highly irregular to nearly even in shape; wall coarsely granular, usually thick, single layered; septa short to long, show slight to moderate anterior direction; coiling plectogyroid, showing large to moderate total angular distortion; aperture narrow, usually low at base of apertural face; mature shells rarely show more than two volutions.

Occurrence.—*Granuliferella* is abundantly distributed throughout Osagian limestone of central Utah and eastern Nevada.

Discussion.—*Granuliferella* differs from *Plectogyra* by its granular, single layered wall, larger proportional chamber size, and small number of volutions.

GRANULIFERELLA GRANULOSA E. J. Zeller

Text-fig. 4—1

Pl. 99, figs. 7,8,12,14

Description.—Shell small, discoidal, involute, more umbilicate on one side than the other, adults average slightly less than 0.4 mm. in diameter; chambers large in comparison to size of shell, not all uniform in shape, individual chambers moderately to slightly inflated; septa long, leave low tunnel, show moderate anterior direction; wall granular, thick in comparison to size of shell, single layered; secondary deposits absent; coiling plectogyroid, showing large angular distortion; two volutions or less in

adult shells; proloculus small; aperture low at base of apertural face.

Occurrence.—*Granuliferella granulosa* occurs abundantly in upper Gardner limestone of central Utah and Joana limestone of western Utah and eastern Nevada.

Discussion.—*Granuliferella granulosa* differs from *G. asperata* by its thinner wall, more regular chambers and septa, lack of external spines, and greater rotational distortion.

Specimens figured on plate 99 closely resemble those illustrated by E. J. Zeller in his original presentation of the species. Length of septa and irregularity in chamber size are character mentioned here not included in the original description.

GRANULIFERELLA TUMIDA E. J. Zeller
Text-fig. 3—4; pl. 100, figs. 6,7

Granuliferella tumida E. J. ZELLER, 1957, p. 696, pl. 77,81

Description.—Shell discoidal, involute, largest individuals average 0.5 mm. in maximum diameter; chambers large, strongly inflated between sutures; septa somewhat shortened, leave a high tunnel; wall single layered, extremely thin; secondary deposits limited to irregular but usually prominent thickenings on posterior side of each septum; total rotational distortion of spiral moderately small; proloculus moderately large; shells have two to two and one-half volutions.

Occurrence.—*Granuliferella tumida* commonly occurs in the upper Gardner limestone of the Provo Rock Canyon section.

Discussion.—*Granuliferella tumida* differs from *G. granulosa* by its highly inflated chambers, much lower total angular distortion, presence of secondary deposits, and much thinner wall.

GRANULIFERELLA? GRANULELLA, n. sp.
Text-fig. 3—7; pl. 99, figs. 9,10,11,13,18

Description.—Shell discoidal, involute, last two or three chambers becoming uncoiled, form rectilinear uniserial growth, average maximum length of adult shells 0.6 mm.; chambers moderately inflated in both portions of shell, large in comparison to size of shell; septa not long, show little anterior direction, incomplete in uniserial chambers; wall single layered, very thick, coarsely granular; secondary deposits lacking; coiling plectogyroid, shows large angular distortion of spiral; largest shells show two volutions; proloculus small; aperture anterior in last uniserial chamber.

Occurrence.—*Granuliferella? granulella* is a rare form known only from the upper half of the *Granuliferella* zone in central Utah. Similar but not identical uncoiled forms occur in the Joana limestones of Conger Mountain and Ely, Nevada sections.

Discussion.—Individuals of this species removed from disaggregated samples and identified by their surface morphology would probably be placed in the genus *Endothyranella.* On the basis of internal morphology—wall structure, coiling, and proportional chamber size—this species is classed with *Granuliferella.* Without the uniserial chamber growth *G? granulella* can easily be mistaken for *G. granulosa.* Both have a typical thick, granuliferellid wall, plectogyroid coil, and large proportional chambers which identify the genus *Granuliferella.*

GRANULIFERELLA ASPERATA, n. sp.
Text-fig. 3—2, pl. 99, figs. 15,16,17

Description.—Shell discoidal, probably partially evolute, periphery uneven, characterized by irregularly spaced nodes and spines, spines frequently missing, average maximum diameter of adults 0.5 mm.; chambers large, moderately to mildly inflated, highly irregular in shape; septa long, massive, show moderate anterior direction; wall very thick, coarsely granular, agglutinated, consists of organic matter, calcite, and quartz grains; secondary deposits lacking; coiling plectogyroid, shows moderately small angular distortion; adults have one and one-half volutions; aperture high.

Occurrence.—*Granuliferella asperata* is a rare form known to occur only in basal upper Gardner limestone of the Provo Rock Canyon section.

Discussion.—*Granuliferella asperata* differs from *G. granulosa* by its thicker wall, higher aperature, fewer volutions, presence of spines on some individuals, and smaller angular distortion.

Genus PLECTOGYRA E. J. Zeller, 1950

Plectogyra E. J. ZELLER, 1950, p. 3.

Genotype.—*Plectogyra plectogyra* E. J. Zeller.

Description.—Shell discoidal, usually umbilicate on one side only, usually involute, size differential large, individuals range from about 0.3 to 1.3 mm. in diameter; chambers usually swollen between sutures; aperture low and slit-like at the center of the base of the apertural face; tunnel enlarged by resorption, extends back through entire length of coil to proloculus; septa formed by down curving of the wall; wall consists of three primary layers and a fourth secondary layer; coiling plectogyroid with large range of twisting or angular distortion of the spiral; secondary deposits generally resorbed in older chambers, best development in chambers of last volution, particularly the last chamber; proloculus variable in diameter but usually not encountered in thin-sections.

Occurrence.—*Plectogyra* has been found in all Mississippian encrinal limestone of central and western Utah and eastern Nevada.

Discussion.—*Plectogyra* differs from *Endothyra* by having a twisted or plectogyroid spiral. Other morphological features are usually different but may be the same. Generic differentiation is best restricted to presence or absence of the plectogyroid spiral. Morphology of the type species is described at length in the original presentation of the genus (E. J. Zeller, 1950, p. 3).

PLECTOGYRA TUMULA E. J. Zeller
Text-fig. 3—11; pl. 101 figs. 12,14,15; pl. 102, fig. 13.

Plectogyra tumula E. J. ZELLER, 1957, p. 697, pls. 77,79,82.

Description.—Shell discoidal, partially evolute, strongly umbilicate on both sides, average maximum diameter of adults 0.7 mm.; chambers of moderate size, not strongly swollen between sutures; septa long, arcuate, show strong anterior direction; wall layering distinct; secondary deposits consist of a prominent symmetrical to slightly asymmetrical tumula on floor of each chamber, tumuli frequently show little evidence of resorption in early portion of coil, show best in chambers of last volution; coiling plectogyroid with very little angular distortion, some individuals nearly planispiral; largest shells have four to five volutions; proloculus small; aperture low.

Occurrence.—*Plectogyra tumula* is abundantly distributed throughout the upper Gardner limestone of central Utah and Joana limestone of western Utah and eastern Nevada.

Discussion.—*Plectogyra tumula* is easily distinguished from other members of the genus by extensive, prominent tumuli, large number of volutions, and small angular distortion. The specimens illustrated here are noticeably larger than Zeller's (1957, pl. 77,79,82) but similar in all other respects.

PLECTOGYRA TANTALA D. E. Zeller
Text-fig. 3—16; pl. 100, figs. 9,11; pl. 103, figs. 9, 11.

Plectogyra tantala D. E. ZELLER, 1953, p. 195, pl. 27.

Description.—Shell discoidal, probably involute, largest individuals average 0.6 mm. in maximum diameter; chambers high, but not shortened, slightly swollen between sutures; septa long, arcurate, but leave moderately high tunnel; wall not thin, layering distinct; secondary deposits consist of hamulus in final chamber and uniform filling on posterior tip of each septum, bases of hamuli occasionally preserved as tumuli in chambers of last volution; total angular distortion moderately small; three volutions in adult shells; proloculus small; last chamber and hamulus broken away in all known central Utah forms.

Occurrence.—Central Utah specimens of *Plectogyra tantala* are rare and known only from the lower *Endothyra symmetrica* zone in the Provo Rock Canyon section.

Discussion.—*Plectogyra tantala* differs from *P. tumula* by having secondary filling on septa and smaller deposits on chamber floors. Coiling, secondary filling on septa, and chamber floor deposits of these specimens closely resemble those figured by D. E. Zeller (1953, pl. 27, figs. 14 and 16). Difference in peripheral shape is probably due to section orientation.

PLECTOGYRA? GIBBOSA, n. sp.
Pl. 100, figs. 2,3,4,5

Description.—Shell discoidal, probably involute, largest shells average 0.65 mm. in

maximum diameter; chambers small, of uneven size and inflation; septa shortened resulting in high tunnel, show different amounts of anterior direction; wall moderately thin, separation into layers indistinct; secondary deposits confined to massive thickenings on both posterior and anterior sides of septa in last volution; total angular distortion large; aperture of moderate height.

Occurrence.—Plectogyra? gibbosa is known only from the upper *Plectogyra tumula* subzone in the Provo Rock Canyon section.

Discussion.—Plectogyra? gibbosa does not show enough separation of the wall into layers to make classification with *Plectogyra* certain. Its small chambers and relatively large size together with rudimentary separation of the wall into layers are plectogyrid characters. Imperfect separation of the wall into layers may be due to biologic growth rather than poor preservation of the shell.

Plectogyra? gibbosa differs from *Granuliferella granulosa* by having smaller chambers, larger shell, and imperfect separation of the wall into layers.

PLECTOGYRA KLEINA, n. sp.
Text-fig. 3—22; pl. 99, figs. 1,4,6.

Description.—Shell discoidal, involute, umbilicate on one side only, adults small, average 0.27 mm. in maximum diameter; chambers small, slightly inflated, higher than long, last chamber enlarged and elongated in some individuals; septa long, leave very low tunnel, show only slight anterior direction; wall moderately thin; secondary deposits missing or consist of poorly developed discontinuous thickenings on chamber floors; coiling plectogyroid, shows large angular distortion; largest shells have two and one-half volutions; proloculus large in comparison to size of shell; aperture very low.

Occurrence.—Plectogyra kleina is restricted to the lower Great Blue limestone in central Utah.

Discussion.—Plectogyra kleina is readily distinguished from other members of the genus by its small size, small, high chambers, and lacking or poorly developed secondary deposits.

PLECTOGYRA TURGIDA, n. sp.
Text-fig. 3—14; pl. 100 figs. 8,10,14; pl. 101, figs. 11,13.

Description.—Shell discoidal, involute, largest individuals average 0.8 mm. in maximum diameter; chambers large, highly inflated; septa long, arcuate; wall thick, finely granular with large proportion of calcareous cement, plectogyrid layering distinct; secondary deposits lacking; coiling plectogyroid with fairly large angular distortion; adults have two to two and one-half volutions; aperture narrow, low.

Occurrence.—Plectogyra turgida is known only from the Pine Canyon limestone of the Cedar Valley Hills section.

Discussion.—Plectogyra turgida differs from *P. bullata* by its thicker wall, absence of secondary deposits, and larger angular distortion.

PLECTOGYRA BULLATA, n. sp.
Pl. 100, figs. 12,13; pl. 101, figs. 6,8,.

Description.—Shell discoidal, umbilicate on one side only, largest shells average 0.75 mm. in maximum diameter; chambers large, with moderately strong and uneven inflation; septa short, leave high tunnel, show definite but usually small anterior direction; wall extremely thin; secondary deposits occur as thin continuous deposits on chamber floors and prominent deposits on either or both sides of each septum, floor deposits sometime missing; coiling plectogyroid with small angular distortion; adult shells show three volutions; proloculus large; aperture moderately high.

Occurrence.—Plectogyra bullata is known only from the *Plectogyra tumula* subzone of the Provo Rock Canyon section.

Discussion.—Plectogyra bullata differs from *P. turgida* by its much thinner wall, presence of secondary deposits, and smaller angular distortion. *P. bullata* differs from *P. inflata* by having irregular and less inflation of chambers, smaller angular distortion, and fewer volutions.

Genus ENDOTHYRA Phillips

Not *Endothyra* BROWN, 1843, p. 17, pl. 6, fig. 2.
Endothyra PHILLIPS, 1846, p. 277, pl. 7, fig. 1.

Genotype.—Endothyra bowmani Phillips.

Description.—Shall discoidal, usually in-

volute, most forms umbilicate on both sides, size differential large, about 0.4 to 1.4 mm. in diameter; swelling of chambers between sutures range from weak to strong, some species with almost none; septa usually curved downward from outer wall at relatively low angle; wall consists of three primary layers, fourth secondary layer occasionally absent; coiling planispiral; secondary deposits usually consist of hamuli or acanthi on the chamber floors in the last volution, especially the last chamber; proloculus simple, frequently not seen except in well oriented sections; tunnel continuous from aperture to proloculus, slightly higher than aperture, enlarged by resorption.

Occurrence.—*Endothyra* is known from only Osagian and Meramecian rocks in central and western Utah and eastern Nevada.

Discussion.—*Endothyra* differs from *Plectogyra* by having a planispiral coil. All other morphological features may be identical. The description presented here is guided by the current need of separating *Endothyra* from *Plectogyra* in sagittal and axial sections. Previous references by Henbest (1931) and Scott, Zeller, and Zeller (1947) have treated plectogyrids as members of *Endothyra*.

ENDOTHYRA SYMMETRICA E. J. Zeller
Text-fig. 3—17; pl. 101, figs. 7,9,10

Endothyra symmetrica E. J. ZELLER, 1957, p. 701, pls. 75,78,80.

Description.—Shell discoidal, umbilicate on both sides, involute, average maximum diameter of adults 0.6 mm.; chambers show little swelling, periphery almost flat; septa moderately long with slight anterior direction; wall moderately thin with distinct endothyrid layering; secondary deposits consist of single prominent hamulus in final chamber and infrequent hamuli on floors of chambers in last volution; coiling planispiral; proloculus of medium size; three and one half to four volutions in largest shells; septal count, first volution seven, second volution eight, third volution ten, fourth volution eleven; medium rate of expansion of the coil.

Occurrence.—Central Utah forms of *Endothyra symmetrica* are restricted to upper Deseret limestone and lower Humbug formation.

Discussion.—*Endothyra symmetrica* differs from *E. disca* by its larger size, more rapid rate of expansion, and presence of secondary deposits. *E. symmetrica* differs from *E. spiroides* by its more rapid rate of expansion, its less numerous septa, and smaller number of volutions.

ENDOTHYRA DISCA E. J. Zeller
Text-fig. 3—3; pl. 101, figs. 4,5

Endothyra disca E. J. ZELLER, 1957, p. 701, pl. 79,80.

Description.—Shell discoidal, small, probably partially evolute, average maximum diameter of adults 0.4 mm.; chambers moderately swollen between sutures; septa moderately long in comparison to height of chambers, show strong anterior direction; walls thin; secondary deposits absent; coiling planispiral with slight irregularity; proloculus small; adults have three and one half volutions; moderately slow rate of expansion of the coil; aperture very low.

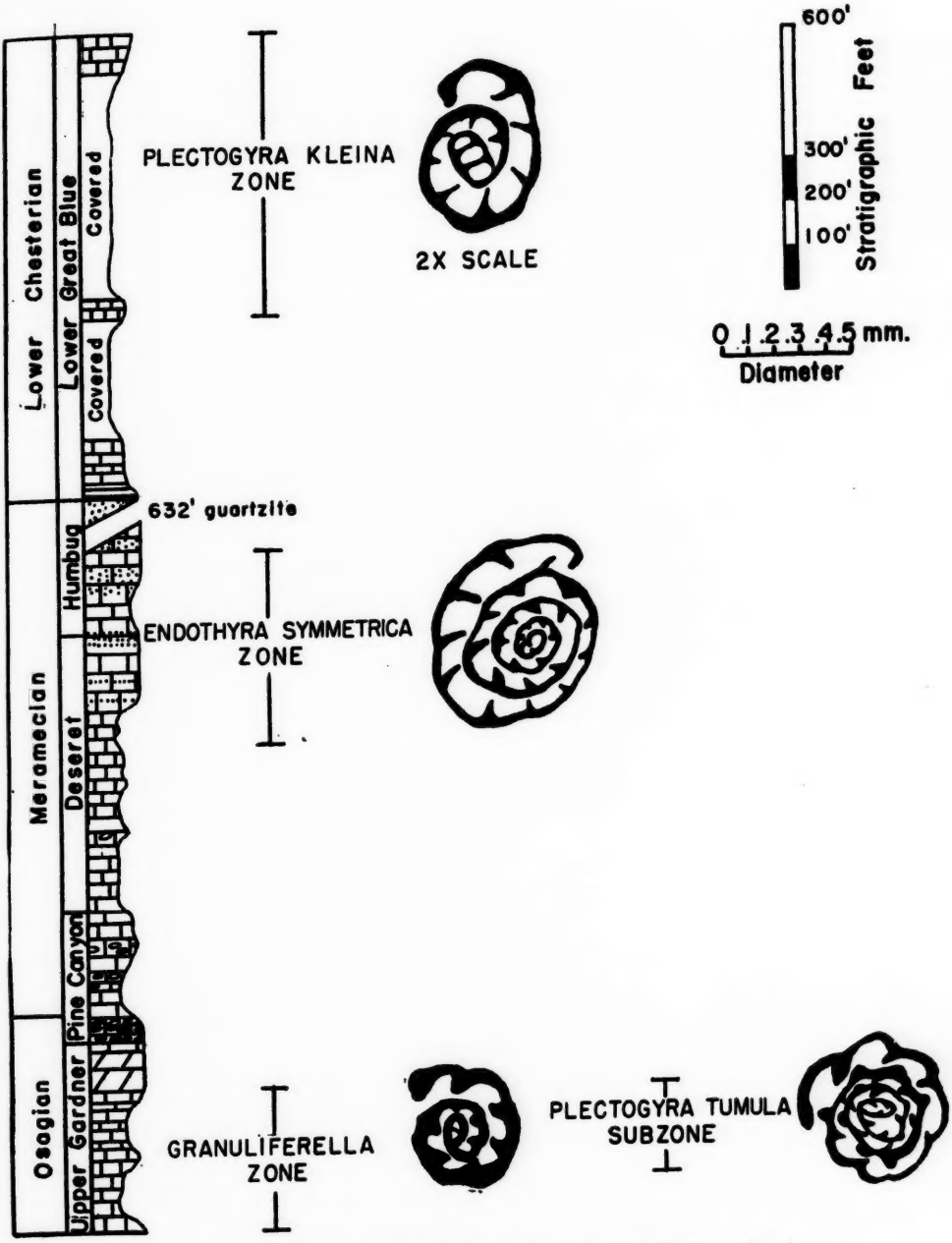
Occurrence.—*Endothyra disca* is known from only the upper half of the *Plectogyra tumula* subzone in Provo Rock Canyon.

Discussion.—*Endothyra disca* differs from *E. taedia* by its longer and less numerous septa, larger chambers, slightly more rapid rate of expansion of the coil, and inflation of the chambers.

ENDOTHYRA? LANCEOLATA, n. sp.
Text-fig. 3—12; pl. 101, figs. 1,2,3

Description.—Shell small, involute, umbilicate on one side only, average maximum diameter of largest shells 0.35 mm.; chambers large in comparison to size of shell, moderately inflated, higher than long; wall thin, distinctly three-layered; septa arcuate, long; secondary deposits confined to massive spearhead shaped growth on last septum apparently giving support to secondary chamber growth; coiling planispiral; proloculus small; coil expands rapidly forming a high apertural face; aperture high.

Discussion.—*Endothyra? lanceolata* differs from all other members of the genus by having only two volutions and a spearhead shaped growth on the last septum. The holotype is the only representative of the genus *Endothyra* known to have a secondary chamber growth.



TEXT-FIG. 2—Stratigraphic zonation of endothyroid Foraminifera in Provo Rock Canyon, Utah County, Utah.

ENDOTHYRA HAMULA, n. sp.
Text-fig. 3—18; pl. 102, figs. 10,11,12

Description.—Shell discoidal, very large, umbilicate on both sides, adults average 1.2 mm. in maximum diameter; chambers very large, show moderately strong swelling between sutures; septa moderately long, show small anterior direction; wall thick, distinctly three-layered; secondary deposits consist of a long curved hamulus in last chamber and roots of hamuli on floor of some chambers in last volution; coiling planispiral with slight irregularity; adults have four to five volutions; coil shows moderately fast rate of expansion.

Occurrence.—*Endothyra hamula* is known only from the upper Deseret limestone of the Provo Rock Canyon section.

Discussion.—*Endothyra hamula* differs from *E. symmetrica* by its larger size, inflated chambers, and shape of the hamulus. *E. hamula* differs from *E. spiroides* by its much greater rate of expansion, less numerous septa, fewer volutions, inflation of chambers, and shape of the hamulus. An individual was not encountered in thin-section that shows septa well enough to give a septal count. The number of septa is estimated to be the same or slightly less than *E. symmetrica.*

ZONATION AND CORRELATION OF CENTRAL UTAH ENDOTHYROIDS

A study of thin-sections of Misissippian rocks in central Utah yields biostratigraphic data on the occurrence of endothyroid foraminifera. Distribution of these foraminifera in the Provo Rock Canyon section suggests four faunal zones represented in text-fig. 2. From the first occurrence upward they are *Granuliferella* zone, *Plectogyra tumula* subzone, *Endothyra symmetrica* zone, and *Plectogyra kleina* zone.

The genus *Granuliferella* is distributed throughout Osagian rocks here represented by the upper Gardner (Madison) limestone. *Plectogyra tumula* is also restricted to Osagian rocks and occurs throughout the upper Gardner limestone within the *Granuliferella* zone. Neither is present above the top of the formation.

The unfossiliferous upper Pine Canyon limestone and lower Deseret limestone are of probable lower Meramecian age, and they separate the Osagian beds from the upper Deseret limestone and lower Humbug formation which are of upper Meramecian age. The *Endothyra symmetrica* zone is limited to encrinal beds of upper Meramecian age. The lower Great Blue limestone of lower Chesterian age consistently contains *Plectogyra kleina.* Microfaunal zonation of upper Chesterian rocks in Provo Rock Canyon is not possible; endothyroids are not known from these rocks.

Abundant individuals belonging to the genus *Granuliferella* are found in the Gardner limestone of the Cedar Valley Hills section and the Joana limestone of the Conger Mountain and Ely, Nevada sections. This conclusively demonstrates a regional distribution of the *Granuliferella* zone from central Utah to eastern Nevada.

EXPLANATION OF PLATE 101
All figures ×50

FIGS. *1–3—Endothyra? lanceolata*, n. sp. Sagittal sections; *1*, the holotype, loc. BYU10991-219, specimen BYU131HT; *2*, loc. BYU10991-219A, specimen BYU160F-A; *3*, loc. BYU10991-219B, specimen BYU161F.

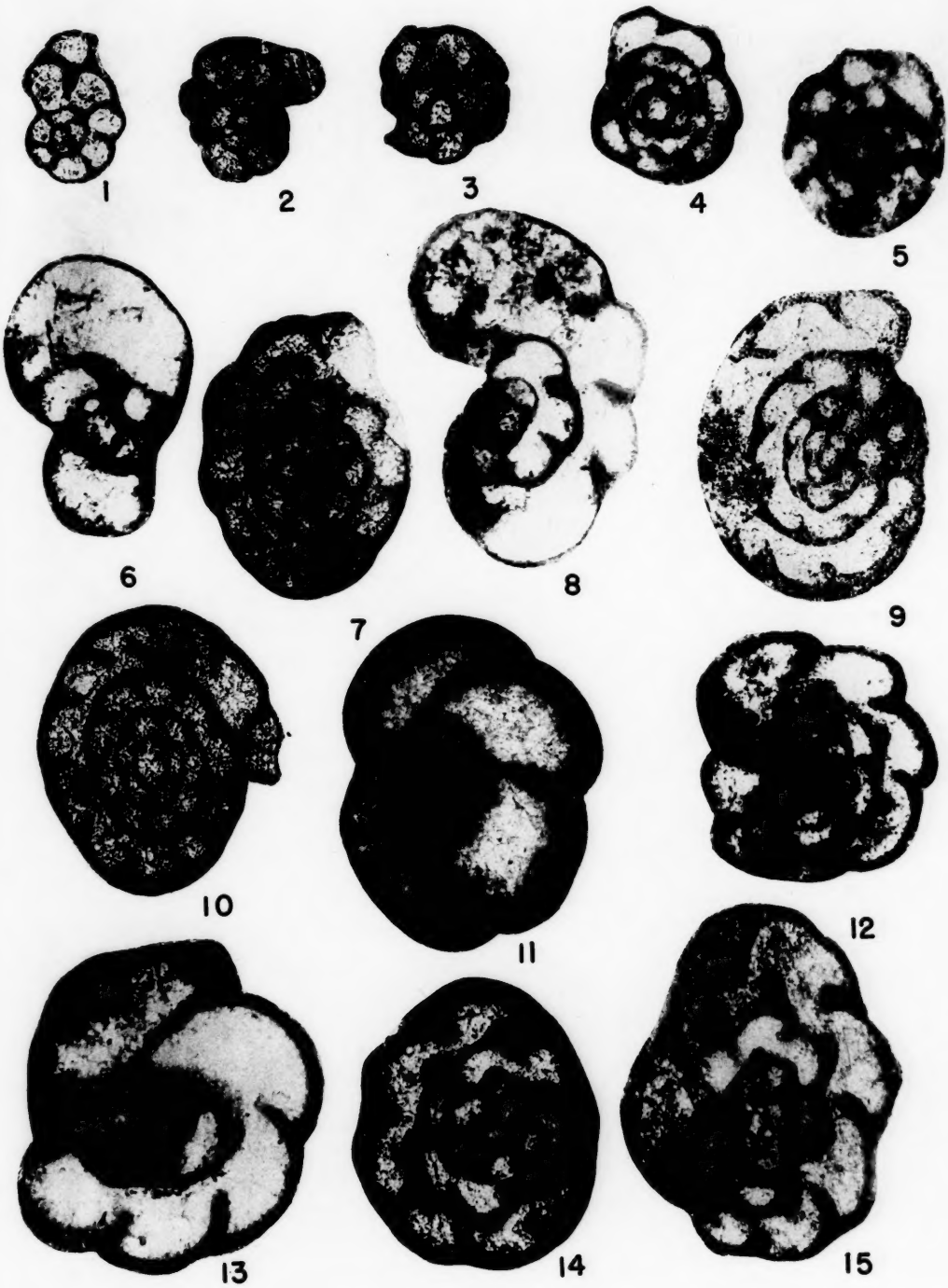
4,5—Endothyra disca E. J. Zeller. Sagittal sections; *4*, loc. BYU10992-551, specimen BYU123F-B; *5*, loc. BYU10992-266, specimen BYU100F-A.

6,8—Plectogyra bullata n. sp. *6*, vertical axial section, loc. BYU10992-322, specimen BYU108F-B; *8*, oblique axial section, loc. BYU10992-322, specimen BYU107F-A.

7,9,10—Endothyra symmetrica E. J. Zeller. Sagittal sections; *7*, loc. BYU10990-388A, specimen BYU162F; *9*, loc. BYU10989-38, specimen BYU154F; *10*, loc. BYU10990-388D, specimen BYU137F.

11,13—Plectogyra turgida, n. sp. *11*, oblique axial section, loc. BYU10983-C, specimen BYU-163F; *13*, the holotype, horizontal axial section, loc. BYU10983-D, specimen BYU133HT.

12,14,15—Plectogyra tumula E. J. Zeller. Horizontal axial sections; *12*, loc. BYU10992-551, specimen BYU124F-C; *14*, loc. BYU10987-M, specimen BYU164F; *15*, loc. BYU10992-274, specimen BYU102F.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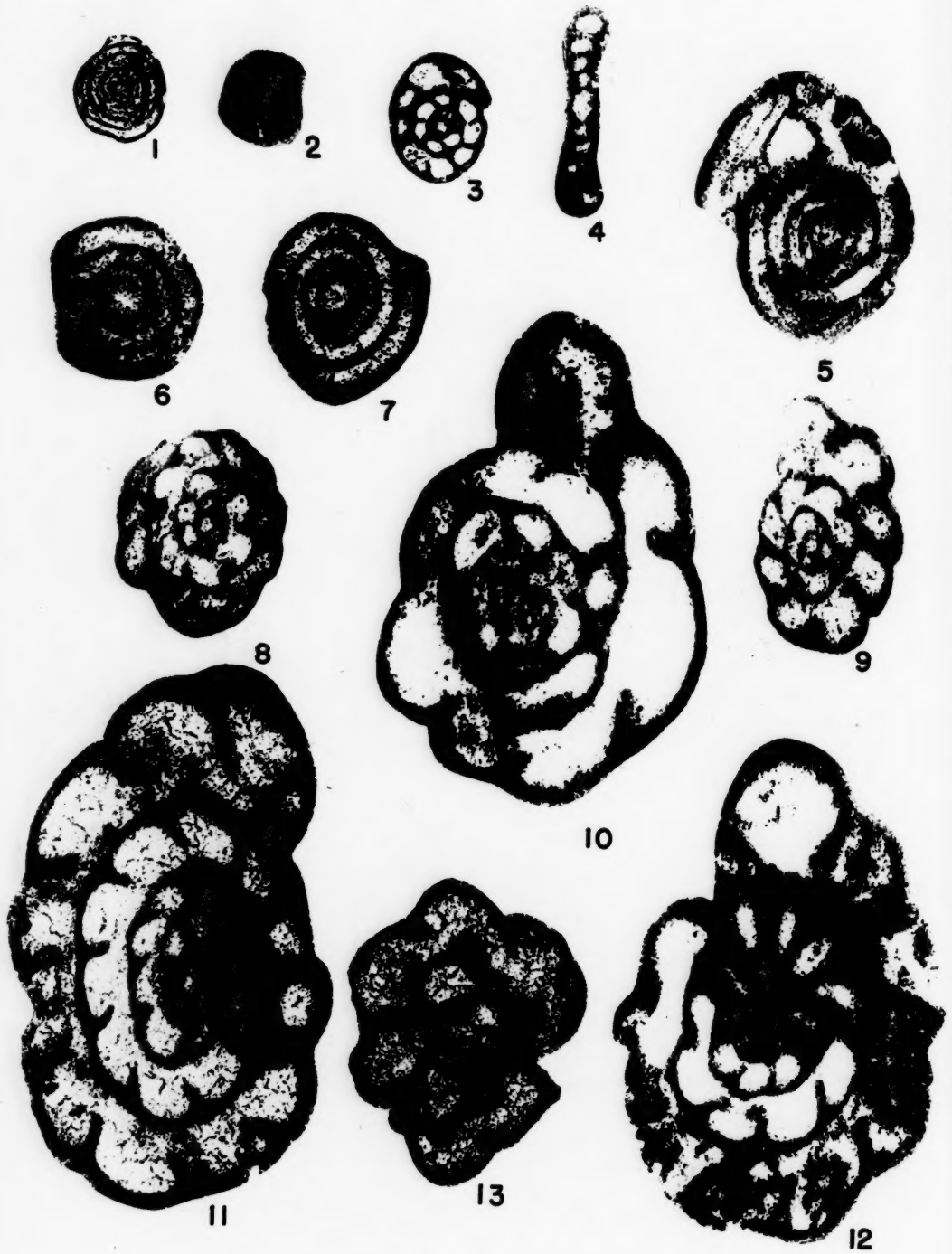
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Representatives of *Plectogyra tumula* were found in the Ely, Nevada section, and is represented by a few poorly preserved individuals in the Cedar Valley Hills and Conger Mountain sections. *Endothyra symmetrica* is similarly rare west of the Provo Rock Canyon section. Zeller (1957, p. 694) reports the occurrence of *Endothyra symmetrica* and *Plectogyra tumula* in the Bear River Range, Cache County, Utah and *Plectogyra tumula* from the south end of the Confusion Range, Millard County, Utah. These occurrences show wide lateral distribution of the *Endothyra symmetrica* and *Plectogyra tumula* zones in northern and eastern Utah.

The *Plectogyra kleina* zone is represented in Great Blue limestone of the Cedar Valley Hills and Provo Rock Canyon sections. Thin-sections of upper Mississippian rocks in the Conger Mountain and Ely, Nevada sections were not prepared, consequently, the occurrence of *Plectogyra kleina* in western Utah and eastern Nevada is not known.

The reason for rare occurrence of zone species west of the type Provo Rock Canyon section is probably not biologic but inadequate sampling and thin-sections. Sampling of sections west of Provo was not systematic. Spot samples taken in these localities were designed to determine approximately lateral distribution of zone species but not vertical distribution.

Faunal control of upper Mississippian strata in western Utah is insufficient to justify an attempt at correlation with the Provo Rock Canyon section. Correlation can be made between lower Mississippian time equivalents.

The Joana limestone contains preponderant *Granuliferella; Plectogyra tumula* is also conspicuous but occurs less abundantly. The occurrence of these faunas strongly suggests the Joana limestone is equivalent to the upper Gardner limestone and should be assigned to the Osagian. Microfaunal evidence can not prove lower Joana beds are upper Kinderhookian. None of the microfauna studied for this paper was collected from rocks known or interpreted to be Kinderhookian.

PHYLOGENETIC TRENDS OF CENTRAL UTAH ENDOTHYROIDS

Endothyroid ancestry.—Plectogyrid phylogeny can reasonably be extended back to unchambered plectogyroid forms belonging to the genus *Glomospira*. Granuliferellids, most primitive of the endothyroids, would be the first derivative of these structurally simple forms. The only morphological changes necessary are the growth of septa and reduction in number of volutions.

With equal reliability the origin of *Endothyra* can be attributed to the chambering and wall structure change of primitive planispiral forms belonging to the genus *Ammodiscus*. If these trends are true, *Plectogyra* and *Endothyra* developed independently making endothyroid phylogeny in central Utah a classic example of parallel evolution.

Known occurrence of *Granuliferella*, *Plectogyra*, and *Endothyra* testifies all three genera were living in association in central Utah when the first endothyroids were buried and preserved. The possibility of investigating a phylogenetic connection be-

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EXPLANATION OF PLATE 102

All figures ×50

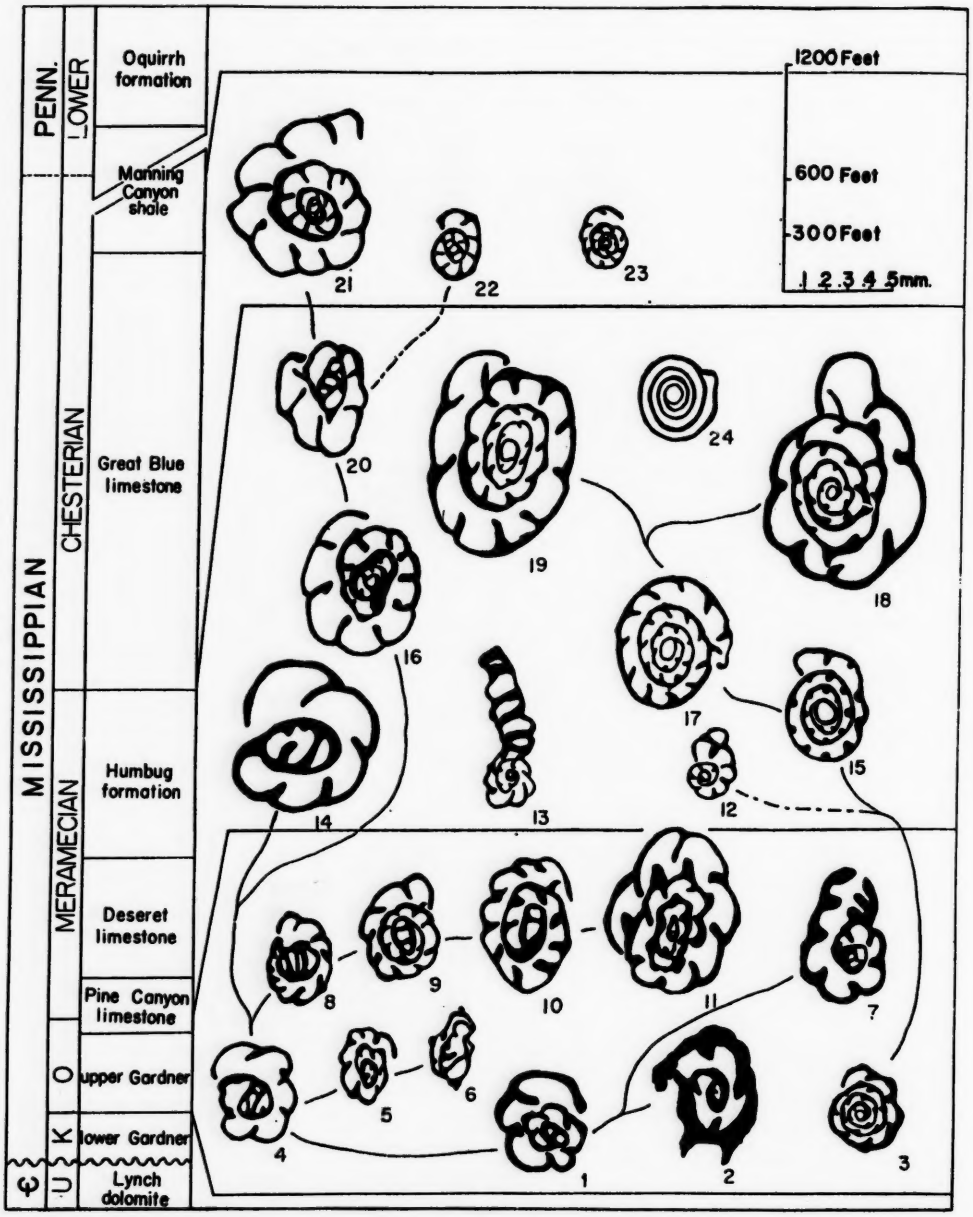
FIGS. *1,2,4–7—Ammodiscus* sp. *1,2,5–7* sagittal sections; *1*, loc. BYU10988-930, specimen BYU165F, *2*, loc. BYU10987-U, specimen BYU166F; *5*, loc. BYU10989-36, specimen BYU168F; *6*, loc. BYU10982-M, specimen BYU169F; *7*, loc. BYU10990-25, specimen BYU146F; *4*; axial section, loc. BYU10989-31, specimen BYU167F.

3—Millerella? sp. Sagittal section, loc. BYU10988-951, specimen BYU145F.

8,9,11—Endothyra sp. Sagittal sections; *8*, loc. BYU10992-322D, specimen BYU119F-C; *9*, loc. BYU10992-322, specimen BYU155F-D; *11*, loc. BYU10990-388B, specimen BYU139F.

10,12—Endothyra hamula, n. sp. Sagittal sections of syntypes; *10*, loc. BYU10990-388, specimen BYU138ST-A; *12*, loc. BYU10990-388, specimen BYU178ST.

13—Plectogyra tumula E. J. Zeller. Offset horizontal axial section, loc. BYU10992-413, specimen BYU121F.



TEXT-FIG. *3*—This is a diagrammatic representation of presumed phylogenetic trends of central Utah endothyroids. Figures 21 and 14 were taken from the Cedar Valley Hills section; the remainder are from the Provo Rock Canyon section. Specimens representative of average forms have been selected and all figures are ×35. *1—Granuliferella granulosa* E. J. Zeller. Horizontal axial section, loc. BYU10992-266, specimen BYU101F-B. *2—Granuliferella asperata* n. sp. Horizontal axial section of holotype, loc. BYU10992-298, specimen BYU104HT. *3—Endothyra disca* E. J. Zeller. Saggital section, loc. BYU10992-551, specimen BYU123F-B. *4—Granuliferella tumida* E. J. Zeller. Horizontal axial section, loc. BYU10992-322, specimen BYU109F-C. *5,6,8–10,20,21—Plectogyra* sp. *5,8–10,20,21* Horizontal axial sections; *5*, loc. BYU10992-290A, specimen BYU128F; *8*, loc. 10992-

tween the planispiral and plectogyroid endothyroids in central Utah will not present itself until Kinderhookian and Upper Devonian faunas are found locally. Thin-sections of lower Gardner encrinal limestones immediately west of Utah Lake may yield data needed to establish this connection.

Light is shed on the conjectural nature of early endothyroid phylogeny in a quotation from E. J. Zeller's (1950, p. 10) publication on Mississippi Valley endothyroids.

> The endothyroids found in Kinderhookian strata are distinct from those of Devonian age both in coiling and structural design of the shell. The first, and probably the most important, single factor which distinguishes the Kinderhookian from the Devonian endothyroid faunas is the total absence of Kinderhookian planispiral forms. All known endothyroids from this part of the lower Mississippian deposits belong to the genus *Plectogyra*.

The complete absence of planispiral endothyroids in Kinderhookian rocks adds weight to the development of plectogyroids through *Glomospira* independent of planispiral influence. In conflict, support is given the development of *Plectogyra* through *Endothyra* by the first appearance of *Endothyra* stratigraphically below *Plectogyra*. *Endothyra* occurs in the Devonian rocks of the Mississippi Valley with the complete exclusion of *Plectogyra* E. J. Zeller (1950, p. 10, pl. 6).

Development of planispiral forms.—Development of planispiral endothyroids in central Utah begins with lower Osagian occurrence of small forms without secondary deposits. This primitive fauna represented by *Endothyra disca* (text-fig. 7—3) gained neither size nor abundance during Osagian and lower Meramecian time.

Meramecian planispiral evolution exploded into a climax of the greatest size and abundance the endothyrids were to develop. The largest endothyroids known from central Utah belong to the genus *Endothyra*. Endothyrid domination of foraminiferal populations in Meramecian seas of central Utah was short lived. Advent of siliceous Humbug (upper Meramecian) sedimentation marked the extinction of the genus *Endothyra* in central Utah for no planispiral endothyroids are known to occur in Chesterian rocks here.

Secondary deposits and size of Meramecian planispiral forms are stratigraphically distinctive. Individuals 1.2 mm. in diameter, on the upper end of the size differential scale, are frequently seen in thin-section. Nearly all Meramecian endothyrids have a prominent hook-shaped hamulus in the final chamber. Some of them grew tumuli and acanthi on chamber floors in the last volution, characters rarely seen in Osagian endothyrids. Characteristic Meramecian endothyrids are represented by *Endothyra hamula*, *Endothyra symmetrica*, and *Endothyra* sp. (text-fig. 3—18,17,19 respectively).

Development of plectogyroid forms.—Plectogyroid evolution, like endothyrid, has its known beginning in central Utah at the base of the upper Gardner (Osagian) limestone. Three Osagian phylogenetic trends from the primitive species *Granuliferella granulosa* can be recognized.

Beginning of the first trend occurs shortly after the appearance of granuliferellids in

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322, specimen BYU110F-D; *9*, loc. BYU10992-551E, specimen BYU129F-E; *10*, loc. BYU10992-322, specimen BYU130F-E; *20*, loc. BYU10990-343, specimen BYU142F; *21*, loc. BYU10980-L, specimen BYU143F; *6*, oblique axial section, loc. BYU10992-290, specimen BYU103F. *7—Granuliferella? granulella*, n. sp. Horizontal axial section of holotype, loc. BYU10992-551B, specimen BYU126HT-B. *11—Plectogyra tumula* E. J. Zeller. Oblique axial section, loc. BYU10992-274, specimen BYU102F. *12—Endothyra? lanceolata*, n. sp. Sagittal section of holotype, loc. BYU10991-219, specimen BYU131HT. *13—Ammobaculites?* sp. Longitudinal sagittal section, loc. BYU10991-219A, specimen BYU132F-B. *14—Plectogyra turgida*, n. sp. Horizontal axial section of holotype, loc. BYU10983-D, specimen BYU133HT. *15,19—Endothyra* sp. Sagittal sections; *15*, loc. BYU-10990-317, specimen BYU134F; *19*, loc. BYU10989-16, specimen BYU141F. *16—Plectogyra tantala* D. E. Zeller. Horizontal axial section, loc BYU10990-278, specimen BYU135F-A. *17—Endothyra symmetrica* E. J. Zeller. Sagittal section, loc. BYU10990-388D, specimen BYU137F. *18—Endothyra hamula*, n. sp. Sagittal section of a syntype, loc. BYU10990-388, specimen BYU138ST-A. *22 Plectogyra kleina*, n. sp. Horizontal axial section of holotype, loc. BYU10988-341, specimen BYU-144HT. *23—Millerella?* sp. Sagittal section, loc. BYU10988-951, specimen BYU145F. *24—Ammodiscus* sp. Sagittal section, loc. BYU10989-25, specimen BYU146F.

lower Osagian and results in a massive thickening of single layered, coarsely granular walls, development of highly irregular septation, and growth of external spines. These irregular granuliferellids are represented by *Granuliferella asperata* (text-fig. 3—2).

The second trend resulted in development of uncoiled forms. These forms are represented by *Granuliferella? granulella* (text-fig. 3—7) and can easily be traced back to *Granuliferella granulosa*. The only difference between them is the growth of two or three uniserial chambers on the uncoiled species. Both have granuliferellid walls and the same plectogyroid coiling habit.

The third Osagian trend involves a phylogenetic transition between the granuliferellids and plectogyrids. Osagian granuliferellids represented by *Granuliferella tumida* (text-fig. 3—4) are small, have large highly inflated chambers, and small number of volutions. The only significant structural difference between the granuliferellids and primitive plectogyrids is the separation of the plectogyrid wall into layers. From these primitive forms, plectogyrid phylogeny shows two additional Osagian trends and a third goes into the Meramecian.

One of the Osagian plectogyrid trends represented by *Plectogyra tumula* (text-fig. 3—11) and *Plectogyra* spp. (text-fig. 3—8,9, 10) immediately developed into a group intermediate on the size differential scale but having the greatest abundance and variety of form displayed by any endothyroid population. *Plectogyra tumula* is taken as the end product in this trend moving toward increased number of volutions, development of tumuli, and reduction in angular distortion.

The other Osagian trend emanating from the granuliferellids resulted in degeneration of size and finally development of spines in at least one species. These small adults shown as *Plectogyra* spp. (text-fig. 3—5,6) are on the lower end of the size differential scale, average 0.4 mm. in maximum diameter, and are an insignificant part of Osagian endothyroid populations.

Meramecian plectogyrids branch from Osagian granuliferellids in two major categories. One of these, represented by *Plectogyra turgida* (text-fig. 3—14), died out early in Meramecian. This trend shows a simple increase in size and separation of the wall into layers with no change in the structural design of the shell.

The other group of Meramecian plectogyrids evolved into populations showing a marked increase in number of volutions, size, and chambers per volution, accompanied by a reduction in the relative size of each chamber. Secondary deposits in these enlarged plectogyrids usually consist of continuous thickenings on the chamber floors and hamuli in the last chambers. All Post-Osagian plectogyrid populations are impoverished.

The trend established by large plectogyrids in Meramecian continued into Chesterian and is represented in the collected fauna by a single specimen from Cedar Valley Hills, *Plectogyra* sp. (text-fig. 3—21).

Lower Chesterian populations are dominated by small forms similar to *Plectogyra kleina* (text-fig. 3—22). Most of the primitive plectogyroid characters seen in Osagian forms are retained in the Chesterian phylogeny of small forms. These minute adults have only two and one half to three volutions. The only advanced characters they have are a plectogyrid wall and a relatively large number of chambers.

Phylogenetic ancestry of these small Chesterian plectogyrids is difficult to determine. They seem to be closely related to primitive Osagian forms rather than highly developed Chesterian or Meramecian types. This may not be true. Small transitional forms should be found in Meramecian rocks. Extensive thin-sectioning of upper Deseret and lower Humbug encrinal limestones failed to yield them. Tentatively, small Chesterian plectogyrids are considered a result of degeneration in highly developed Meramecian or lower Chesterian populations.

CORRELATION WITH MISSISSIPPI VALLEY ENDOTHYROIDS BY COMPARATIVE PHYLOGENY

The evolutionary development of Mississippi Valley endothyroids presented by E. J. Zeller (1950, pl. 6) has several trends similar to the phylogenetic development of faunas in central Utah. The most significant and most obvious relationship is the development of large planispiral forms in the Meramecian from both basins. The Meramecian

of Mississippi Valley has large planispiral endothyroids similar to *Endothyra symmetrica*. Another striking similarity occurs in the genus *Plectogyra*. Meramecian plectogyrid populations in both areas show marked advance in size, number of volutions, and development of secondary deposits different from those seen in the Osagian. One central Utah Meramecian plectogyrid is identical to *Plectogyra tantala* in specific details described by D. Zeller (1953, p. 197, ch. 1) but is considered lower Chesterian in Mississippi Valley.

Lower Chesterian endothyroids also show similarity in phylogenetic development. Both areas are dominated by plectogyrids three to five times smaller than the largest Meramecian endothyroids and have poorly developed secondary deposits. *Plectogyra kleina* (text-fig. 3—22) and *Plectogyra* sp. (text-fig. 3—21) are similar to Chesterian forms of Mississippi Valley illustrated by E. J. Zeller (1950, pl. 6). A key to Chesterian correlation is the association of the fusulinid genus *Millerella* with the plectogyrids in place of true planispiral endothyroids. *Millerella* is difficult to differentiate from *Endothyra*, and the relationship of these genera needs more study.

The progressive development of Chesterian plectogyrids is not as easily followed in central Utah as the seemingly complete Mississippi Valley sequence. Only one large highly developed plectogyrid individual was found in the Chesterian of central Utah and this is more likely a phylogenetic product of similar Meramecian forms than of degenerate Chesterian plectogyrids. The sequence from degenerate to highly developed Chesterian plectogyrids in Mississippi Valley is well illustrated by E. J. Zeller (1950, pl. 6). If additional thin-sections of Chesterian rocks in central Utah yields forms usable in establishing a similar sequence the correlation of Great Blue limestone with Chesterian of Mississippi Valley will be confirmed.

Difficulty is encountered in correlating lower Mississippian phylogenies. The genus *Endothyra* occurs with the first appearance of Osagian in central Utah. In the Mississippi Valley this genus does not occur after its first appearance in the Devonian until Meramecian, leaving Kinderhookian and Osagian rocks devoid of endothyrids (E. J. Zeller, 1950, p. 18, pl. 6). Osagian appearance of planispiral endothyroids in central Utah is explained by considering their small size and primitive undeveloped secondary deposits a necessary requisite for endothyrids occurring stratigraphically below the highly developed Meramecian populations. If planispiral endothyroids are found in the Osagian of Mississippi Valley it is suspected they will be primitive in character similar to the rare Utah forms.

Plectogyroid foraminifera from Osagian rocks of the two areas show few similarities as currently understood. *Plectogyra? gibbosa* of central Utah has unevenly inflated, partially lumpy chambers characteristic of the Mississippi Valley Osagian fauna. This species does not fit into the phylogenetic plan of central Utah forms. Increasing number of volutions, decrease in amount of angular distortion, and development of secondary deposits is a trend easily followed in Central Utah Osagian fauna but not distinguished in Mississippi Valley. The only character these two faunas have in common is intermediate size differential and plectogyroid coiling. Appearance of uncoiled forms and growth of spines on central Utah Osagian forms are also in direct opposition to morphological character of Mississippi Valley plectogyroid faunas.

E. J. Zeller (1950, pl. 6, fig. 3a,b) has placed specimens in uppermost Kinderhookian which bear typical coiling and relative chamber size of *Granuliferella*. Stratigraphy of Mississippi Valley Lower Mississippian is poorly understood and may account for the possible time misplacement of these apparent "granuliferellids." Positive identification will not be possible until wall structure of these specimens is determined. Placing all of Zeller's Humboldt and Gilmore City specimens in the Osagian would allow more similarity between faunas of the two areas than can now be interpreted. Further study of both Mississippi Valley and Utah Osagian endothyroids will undoubtedly yield a better correlation than is now understood. The correlation of upper Gardner limestone with Osagian strata of the type Mississippi Valley rocks is based on predicted similar phylogeny and relative stratigraphic position rather than on certainty of known similar phylogeny.

Furthermore, absence of endothyroids in lower Gardner dolomite makes correlation of this part of the section based on microfaunal populations impossible. Its relative stratigraphic position below Osagian (upper Gardner limestone) suggests a Kinderhookian age.

Correlation by phylogeny is aided by biologic unconformities or breaks in phylogenetic development among populations representing each epoch. A major change in phylogenetic development occurs at the contact of each epoch in both Mississippi Valley and central Utah. A biologic unconformity similar in magnitude and character development to the Mississippi Valley Meramecian-Chesterian break occurs between the base of the Great Blue limestone and beginning of the siliceous Humbug rocks. This places the Meramecian-Chesterian contact in central Utah within the upper Humbug formation or possibly at the Great Blue-Humbug contact.

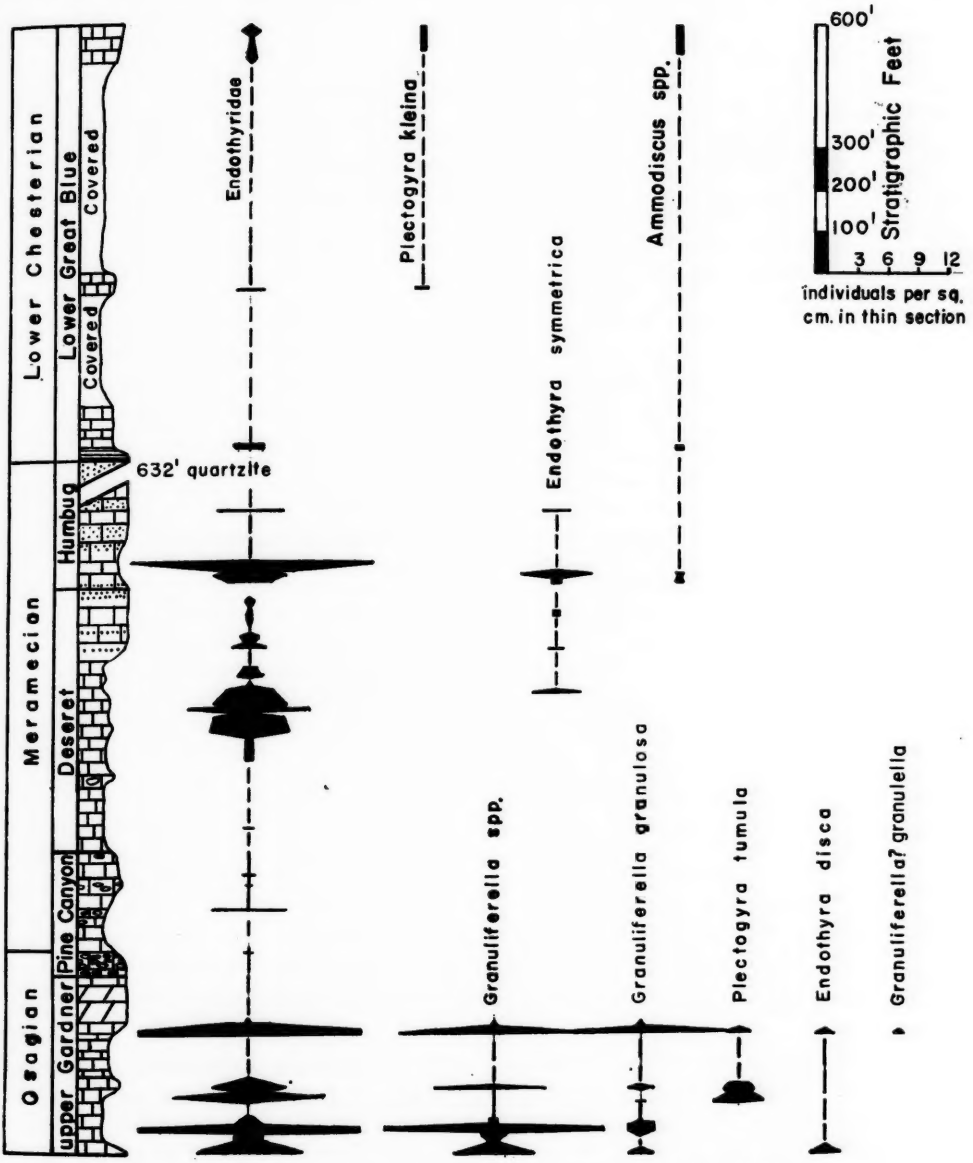
The most marked biologic unconformity in the central Utah sequence occurs within unfossiliferous upper Pine Canyon limestone and lower Deseret limestone and is similar to the Osagian-Meramecian break in character development of the Mississippi Valley. Mississippi Valley and central Utah populations on the Osagian side of this unconformity differ from each other in both specific details and phylogenetic development. However, the strong phylogenetic break is obviously present in both areas and outweighs the negative value of dissimilarities in the Osagian populations from the two areas.

ECOLOGIC INTERPRETATIONS

Abundance distribution, lithologic association, and biologic factors.—Endothyroids occur in greatest abundance in a lithology of fossil hash of coarse echinoderm fragments with a calcarenite or calcirudite groundmass. Reference to text-fig. 4 shows their abundance in encrinal rocks. They were apparently sensitive to environment, for either a change in composition or texture of the enclosing rock shows striking reduction in abundance. Endothyroids are absent in the dolomitic rocks of Provo Rock Canyon. The Pine Canyon limestone and lower Deseret limestone characteristically have a fine grained groundmass containing minor amounts of echinoderm fragments and sponge spicules. Endothyroid foraminifera are represented in these formations by only a few rare uncoiled forms and small polectogyrids, possibly infants. Fossils of microorganisms are completely lacking in thin-sections of quartzite and calcareous sandstone of the middle and upper Humbug formation. Endothyroids are not found in central Utah after beginning of the dense carbonaceous and carbonate mud sedimentation of the middle and upper Great Blue limestone.

The granular wall of the granuliferellids shows a range of selective agglutination and these forms can be accepted as bona fide vagrant benthonic. The plectogyrids and endothyrids have a large amount of calcareous cement in their walls and can be placed in a benthonic environment also but with less certainty. Pelagic or planktonic foraminifers are expected to be widely dispersed and transported into a great variety of sedimentary burial grounds without regard to biotopic conditions. As stated earlier these microfossils occur only in encrinal rocks with calcarenaceous or calcirudaceous groundmass. Limited biocoenosic association with echinoderm fragments and lithologic association of mild current bedding clearly indicate a benthonic habitat for all central Utah endothyroids in marine water shallow enough to permit rudimentary sorting and fragmentation of the sedimentary interface. Occurrence of endothyroids as nuclei in oolitic grains of upper Deseret and lower Humbug rocks is strong evidence of sorting and shifting after death but does not necessarily indicate subsequent widespread geographic distribution.

Encrinal rocks with fine grained groundmass commonly contain small endothyroids in rare occurrence and less commonly in moderate abundance. The indiscriminate dispersal of small forms in both coarse and fine grained sedimentary environments is indicative of pelagic or planktonic habit, possibly during an immature stage of growth. Planktonic or pelagic habit during infancy is usable but not necessary in accounting for the extensive geographic distribution of endothyroid faunas. Violent storm currents and slow migration are sufficient to distrib-



TEXT-FIG. 4—Abundance of distribution of endothyroid Foraminifera in Provo Rock Canyon, Utah County, Utah.

ute vagrant benthonic microorganisms over large areas.

Care must be taken in accounting for absence of planktonic or pelagic infants in chemically unsuitable rocks. A swarm of sensitive infants floating into magnesium-charged waters would be catastrophically killed and become part of the ensuing dolomitic rock. Endothyroids, infant or adult, do not occur in dolomitic, highly carbonaceous, or siliceous sediments.

The most probable answer is to consider small forms in the fine-grained Pine Canyon and lower Deseret limestones as adults well

adapted to deep water living in thinly populated biotopes as compared to the copious populations living among fragmenting echinoderms on a marine shelf subject to mild current action.

Abundance data and flood occurrence.—Sampling and thin-sections done without systematic procedure will not yield reliable abundance data. Text-figure 5 was prepared to show variation in abundance with series sections. Five samples were selected for study representing flood occurrence of endothyroid foraminifera. Estimating an average interval of one centimeter, a series of thin-sections was prepared of each sample and the number of individuals counted. A large viariation in abundance with stratigraphic distance in centimeters demonstrates the inaccuracy of determining abundance data from only one thin-section of each sample. Text-figure 5, sample number BYU 10992-551, shows that at least ten sections are needed to obtain accurate abundance occurrence data in samples with considerable abundance variation.

Interval sampling does not represent all the rocks of any stratigraphic sequence, but a sample covering three to four stratigraphic inches taken at intervals of every two to three feet is considered sufficient to represent abundant populations. Some of the sections from samples on text-fig. 5 show as many as three genera with a total of eight to twelve species. Frequently, rare individuals occur on only one thin-section, even of samples serially sectioned. This is expected because the chance of encountering rare forms on sections representing a minute fraction of the total sample volume is remote. Samples would probably show a greater variety of forms if they could be disaggregated and all individuals removed for observation.

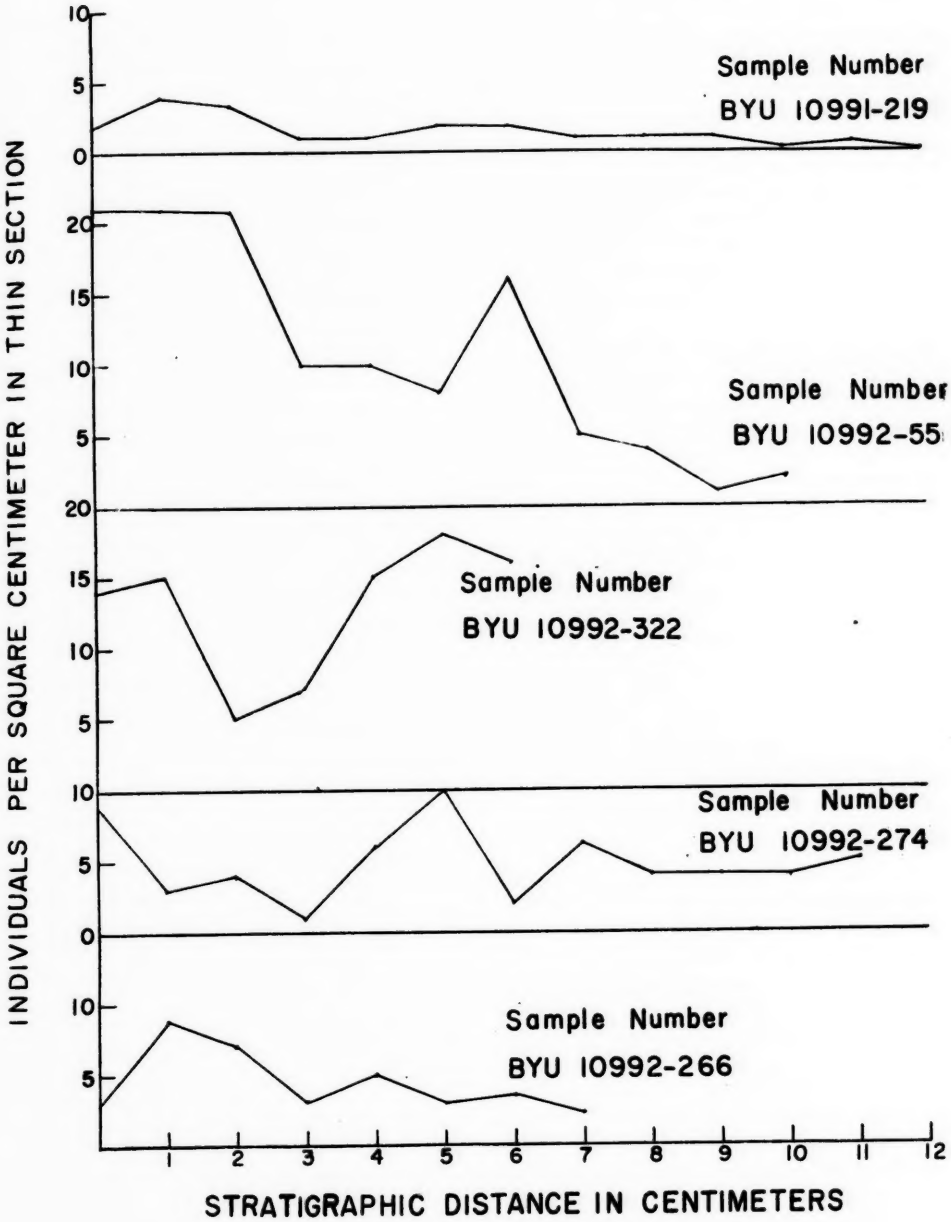
Flood abundance is not known to occur above the Osagian of the samples studied and consequently unimportant with respect to total occurrence. However, flood abundance represents some sedimentary, ecologic, and biologic conditions worthy of note. Five hypotheses are presented to account for the preponderant (see text-figs. 4,5, for graphic representation of flood abundance) occurrence of lower Mississippian foraminifera.

The first is biologic. Endothyroids may have lived and died in periodic or seasonal broods or swarms to become entombed in sediments at stratigraphic intervals measurable in centimeters.

The second hypothesis is ecologic. Populations, sensitive to environment, may have been subjected to periodic change in temperature, salinity, and sedimentary composition of particles suspended in sea water causing death to overtake large numbers catastrophically. Evidence of endothyroid sensitivity to environment is indicated by their diminished abundance or complete absence in rocks of non-calcareous composition and non-encrinitic texture. Unfortunately, lithology does not aid in determining sensitivity to unpreservable factors of temperature, salinity, and composition of suspended particles in the sea water. It seems likely that if they were sensitive to some environmental factors they would also be sensitive to others.

Sedimentary sorting is the third hypothesis but evidence is not in favor of this having an effect on flood occurrence. Sedimentary sorting assumes endothyroids lived in a variety of environments and were transported between the time of death and burial to a previously selected encrinal burial ground. This could happen to pelagic or planktonic foraminifers subject to current action but not to endothyroids. Cross bedding and sorting is not observed in association with flood occurrence. Current bedded, sorted, and abraided encrinal rocks show a strong tendency to have impoverished microfossil populations. Vigorous current action is considered negative influence on flood occurrence of endothyroid foraminifera.

Euhedra and subhedra of calcite are frequently associated with flood abundance of endothyroids in the groundmass of Osagian encrinal limestones. Secondary crystal growth after deposition is expected to corrode and displace fossil material in contact with crystal faces. None of the effects of recrystallization are observed in the limestones. In spite of the difficulty of such crystals growing contemporaneous with the accumulation of organic debris, such as that found in encrinal limestones evidence leaves no other conclusion plausible. Moore (1957, p. 109,110) observed these crystals from the Pierson and Reed Spring formations of northcentral Arkansas. He concluded that



TEXT-FIG. 5—Variation in absolute abundance with series based on thin sections from Provo Rock Canyon.

these crystals could not have been introduced long after sedimentation, but felt uncertain, as does the writer, that they grew contemporaneous with accumulation of the associated organic debris. These crystals provide further evidence sedimentary sorting had a negligible influence on flood occurence. One can hardly conceive of such crystals growing at a sedimentary interface disturbed by vigorous current action.

Differential preservation is the fourth hypothesis and may be a significant influence on flood occurrence. Thin-sections of samples showing a dim outline of abundant poorly preserved endothyroids stratigraphically alternate with samples showing well preserved populations. Poor preservation is common and can easily give the illusion of diminished abundance. Samples showing poorly preserved fossils are usually weathered. Collection of unweathered samples is necessary to be certain the microfauna was not destroyed by that process. Evidence indicates post-depositional changes in the sediments had influence on differential preservation.

The fifth hypothesis proposes the synchronous working of biologic, ecologic, and sedimentary factors in periodically killing and preserving swarms of endothyroid populations. It is illogical to think that all biotopic factors did not influence the mode of preservation of micro-organisms living in an ancient shallow sea. It is satisfactory to think some factors may have had more influence than others. Endothyroid sensitivity to environment has been previously pointed out. The slightest change in environmental conditions may have overcome populations and caused them to die en masse.

SUMMARY

Distribution of endothyroid foraminifera in the Mississippian rocks of Provo Rock Canyon suggests three faunal zones and one subzone. Form the base up these are: *Granuliferella* zone, *Plectogyra tumula* subzone, *Endothyra symmetrica* zone, and *Plectogyra kleina* zone.

The genus *Granuliferella* has wide geographic distribution in upper Gardner (Madison) limestone of central Utah and the Joana limestone of western Utah and eastern Nevada. *Plectogyra tumula* is also restricted to Gardner limestone and its equivalents but occurs with much less abundance than *Granuliferella*. Neither is present above the top of the formation.

The unfossiliferous Pine Canyon and lower Deseret limestones are of lower Meramecian age and they separate the Osagian beds from the upper Deseret limestone and lower Humbug formation which are of upper Meramecian age. *Endothyra symmetrica* abundantly occurs within the encrinal upper Meramecian rocks of central Utah.

The lower Great Blue limestone of lower Chesterian age consistently contains *Plectogyra kleina*. There is no observed occurrence of endothyroid foraminifera in upper Chesterian rocks.

Structure of shell wall, abundance, size, secondary deposits, and variation in coiling show phylogenetic change through time and can be used as stratigraphic indicators with the zonation. Osagian rocks show the greatest abundance and diversity of form of any endothyroid population. Granuliferellids and some of the uncoiled forms are the only endothyroids with a thick, granular, single layered wall. With few exceptions this character is limited to Osagian rocks. The largest endothyroids known are found in Meramecian strata and belong to the genus *Endothyra*. Both *Plectogyra* and *Endothyra* in Meramecian rocks display the most advanced development of acanthi and hamuli seen in any endothyroid assemblage. Chesterian plectogyrids are impoverished and small adults dominate the populations. The fusulinid genus *Millerella* occurs in the place of planispiral endothyroids in Chesterian rocks.

Lithologically, endothyroids occur in greatest abundance in a fossil hash of coarse echinoderm fragments with a calcarenite or calcirudite groundmass. They were apparently sensitive to environment for either a change in composition or texture of the enclosing rock shows a striking reduction in their abundance. Endothyroids are absent from the dolomitic rocks of the lower Gardner dolomite. The Pine Canyon and lower Deseret limestones characteristically have a fine grained groundmass containing minor amounts of echinoderm fragments and sponge spicules. Endothyroid foraminifera are represented in these formations by only a few rare uncoiled forms and small plectogyrids. Microorganisms are completely absent in the quartzite and calcareous sandstone of the middle and upper Humbug formation. Endothyroids are not observed to occur in the dense carbonaceous and carbonate mud sediments of the middle and upper Great Blue limestone.

Irregularity in form, granular wall of individuals, lithologic association with

echinoderm stem segments, and current bedding indicate a benthonic habit during life in sea water shallow enough to permit rudimentary sorting.

Flood occurrence of endothyroids is attributed to the synchronous working of biological, ecological and sedimentary factors in killing and preserving sensitive populations en masse. Textural association of endothyroids with unbroken echinoderm stem segments and whole macrofossils remove weight placed on sedimentary sorting as an influence on flood occurrence.

Subhedra and euhedra of calcite in the groundmass of encrinal limestone is not clearly understood but may have grown contemporaneous with sedimentation.

COLLECTING LOCALITIES

A locality number for each sampled formation has been assigned by the Brigham Young University repository, and each specimen in the Explanation of Plates is stratigraphically identified with this number. Samples from the Provo Rock Canyon section are followed by a number indicating stratigraphic feet above the base of the locality. For example, sample BYU 10992-551 was collected in locality BYU 10992 and 551 stratigraphic feet above the base of the upper Gardner limestone. Locality numbers of the other stratigraphic sections are followed by a letter L, M, or U (lower, middle, or upper) indicating estimated stratigraphic position within a formation.

Some samples have more than one thin-section with illustrated specimens. These thin-sections are differentiated by adding A, B, or C . . . to the locality number. Specimen numbers are followed by F, HT, or ST (figure, holotype, or syntype). Individuals from a thin-section having more than one illustrated specimen are differentiated by adding A, B, or C . . . to the specimen number.

BYU 10992. Upper Gardner limestone, Provo Rock Canyon; SW¼ sec. 28, T. 6 S., R. 3 E.; Cambrian Lynch dolomite-Mississippian Gardner dolomite unconformity marked (Cl-MgO′) on the north canyon wall in nearly vertical strata about 30 feet west of the first wooden bridge and 40 feet above the creek bed.

Samples BYU 10992-266 to -423 collected in saddle above talus cover on north canyon wall; lower Gardner dolomite-upper Gardner limestone contact marked (MgL-MgU 266′) at lower end of saddle.

Samples BYU 10992-551 to -575 on south canyon wall about 5 feet above stream bed; number 551 is clearly visible from the second wooden bridge looking south toward the canyon wall about 5 feet above the stream bed.

BYU 10991. Pine Canyon limestone, Provo Rock Canyon; SE¼ sec. 28, T. 6. S., R. 3 E.; Gardner dolomite-Pine Canyon limestone contact marked (Mg 685′-Mpc O′) on north canyon wall 5 feet above the stream bed and about 50 feet east of the second wooden bridge.

Samples BYU 10991-4 to -254 collected from north canyon wall 5 to 15 feet above stream bed.

BYU 10990. Deseret limestone, Provo Rock Canyon; SE¼ sec. 28, T. 6 S., R. 3 E.; Pine Canyon limestone-Deseret limestone contact marked (Mpc 293′-Md O′) at lower end of saddle on prominent, thin bedded, dark blue and smooth weathering slope zone on the north canyon wall above talus cover.

Sample BYU 10990-53 collected from a thin ledge forming bed in the slope zone.

Samples BYU 10990-222 to -278 collected in cliffs, above talus cover, shedding light grey, blocky weathering, coarse encrinites; cliffs are on north canyon wall above talus cover where the sequence is continuously exposed.

Samples BYU 10990-291 to -319 collected from traverse offset 25 yards up apparent dip from BYU 10990-278.

Samples BYU 10990-333 to -343 collected from traverse offset 40 yards up apparent dip from BYU 10990-333.

Samples BYU 10990-388 to -593 collected from traverse offset up apparent dip from BYU 10990-388.

BYU 10989. Humbug formation, Provo Rock Canyon; NE¼ sec. 28, T. 6 S., R. 3 E.; Deseret limestone-Humbug formation contact marked (Md 639′-Mh O′) at upper end of Deseret limestone traverse at base of prominent quartzite cliffs on north canyon wall.

Samples BYU 10989-16 to -187 collected in traverse offset 40 yards down apparent dip from contact marker to avoid vertical cliffs.

BYU 10988. Great Blue limestone, Provo Rock Canyon; NE¼ sec. 28 and NW¼ sec. 27, T. 6 S., R. 3 E.; Humbug formation-Great Blue limestone contact marked (Mh 886′-Mgb O′) on a nearly east-west trending ridge at a point 850 feet northwest from the intersection of Rock Canyon and First Left Fork; formational contact on the ridge recognized by a lithologic change from an 8 foot bed of Humbug quartzite to shale in basal Great Blue; 2 foot bed of limestone separates the quartzite and shale.

Samples 10988-24 and -26 collected from the dip slope on the southwest side of the First Left Fork of Rock Canyon.

Sample 10988-341 collected from a 2 foot discontinuous outcrop at the base of the slope on the northwest side of the First Left Fork of Rock Canyon.

Samples 10988-884 to -976 collected in prom-

inent cliffs above talus and vegetative cover on the northeast canyon wall of the First Left Fork of Rock Canyon; traverse at the base of the cliffs located 1250 feet south of the north line, 350 feet west of the east line, sec. 28, T. 6 S., R. 3 E.

BYU 10987. Joana limestone, Conger Mountain; collected on east flank of Conger Anticline, Fish Springs quadrangle, 0.6 miles east of 113° 45′ meridian, 4.7 miles south of 39° 15′ parallel, and 2.8 miles southwest from the peak of Conger Mountain.

BYU 10986. Chainman shale, Conger Mountain; collected in encrinal beds 500 feet northeast up the spur from Conger Springs, Fish Springs quadrangle.

BYU 10985. Joana limestone, Ely, Nevada; collected in a section northeast of type area, one mile northwest of junction of Ruth Road with U. S. Highway 50, 5 miles northwest of Ely, Nevada.

BYU 10984. Upper Gardner limestone, Cedar Valley Hills; NW¼ sec. 32, T. 6 S., R. 1 W.; collected at base of first significant spur north of Cedar Valley Rock Canyon.

BYU 10983. Pine Canyon limestone, Cedar Valley Hills; NW¼ sec. 32, T. 6 S., R. 1 W.; collected stratigraphically above and on the same spur as BYU 10984.

BYU 10982. Deseret limestone, Cedar Valley Hills; SE¼ sec. 29, T. 6 S., R. 1 W.; collected topographically above and on the same spur as BYU 10984.

BYU 10981. Humbug formation, Cedar Valley Hills; SW¼ sec. 29, T. 6 S., R. 1 W.; collected topographically above and on the same spur as BYU 10984 and from west side of hill with 5995 feet maximum elevation.

BYU 10980. Great Blue limestone, Cedar Valley Hills; NE¼ sec. 32, T. 6 S., R. 1 W.; collected from northwest slope of hill capped by northeast trending ridge with maximum elevation of 5986 feet.

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MANUSCRIPT RECEIVED JANUARY 2, 1958

EXPLANATION OF PLATE 103

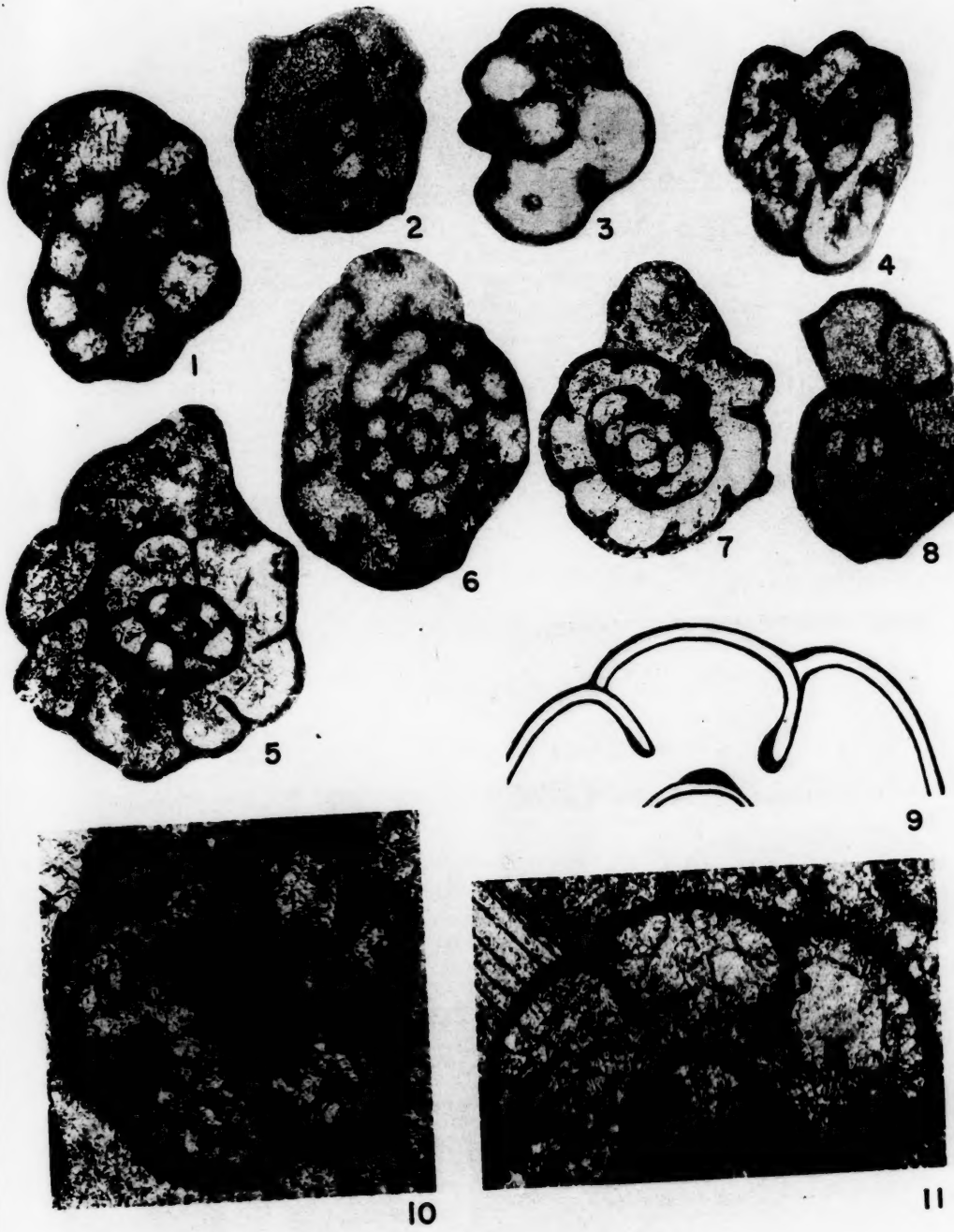
Figures 1–8 ×50; 9–11 ×100

FIGS. *1–5,7,8—Plectogyra* spp. Horizontal axial sections; *1*, loc. BYU10983-A, specimen BYU171F; *2*, loc. BYU10992-278, specimen BYU172F-B; *3*, loc. BYU10992-322C, specimen BYU116F-D; *4*, loc. BYU10990-343, specimen BYU142F; *5*, loc. BYU10980-L, specimen BYU143F-A; *7*, loc. BYU10989-45, specimen BYU176F; *8*, loc. BYU10990-278B, specimen BYU177F.

6—Endothyra sp. Sagittal section, loc. BYU10990-388C, specimen BYU175F.

9,11—Plectogyra tantala D. E. Zeller. *9*, sketch of figure *11* showing wall structure; *11*, greatly enlarged section of part of fig. *9*, pl. *100*, showing endothyrid-plectogyrid wall structure.

10—Granuliferella? granulella, n. sp. Greatly enlarged section of part of fig. *9*, pl. *99*, showing granuliferellid wall structure.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JOURNAL OF PALEONTOLOGY, V. 32, NO. 5, P. 815–837, PLS. 104–106, 3 TEXT-FIGS., SEPTEMBER 1958

SIGNIFICANCE OF EXTERNAL FORM IN SOME ONONDAGAN RUGOSE CORALS

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ABSTRACT—*Part 1:* Rugose corals with elliptical cross-sectional shapes may be defined as depressed or compressed depending on whether the short diameter of the ellipse is in the cardinal-counter plane or perpendicular to it. Various systematic importances have been assigned to the form of the corallum, varying from generic to sub-specific. Treatment varies with authors but also with the groups being studied and each case of compression or depression must be handled on its own merits.

Depressed corals, assignable to two genera are known from Onondagan strata but other examples representing other familes are known from the Ordovician to the Mississippian. Depression in Onondagan corals is considered to be of subgeneric importance and a new subgenus, *Aemulophyllum*, is described.

Compressed corals of Onondagan age are known from 3 genera in 3 families, but several Mississippian examples have been described and Ordovician to Mississippian forms are known. Compression seems to be of subgeneric to subspecific importance in the Devonian groups.

Corallum form may be due to environmental adaptation but seems to be genetic in most of the cases described. Devonian compressed and depressed species have met with little success and are only locally distributed in time and space. Study of both shapes provides excellent examples of homeomorphy in the rugose corals.

Part 2: Little has been done on individual variation in rugose corals from a single horizon and locality. Such a study of some 250 specimens of *Metriophyllum* (*Aemulophyllum*) *exiguum* from the Onondaga limestone in New York has enabled the recognition of 6 formae which form a completely intergradational system. Defining factors are (1) rate of diameter increase relative to length increase, (2) shape of corallum, and (3) size. The variation is possibly due to external factors but is more probably genetic. Individual age is considered unimportant.

EXPLANATION OF PLATE 104

All figures ×1 unless otherwise indicated

FIGS. *1–16—Homalophyllum ungula* (Rominger). *1–3*, counter, cardinal and lateral views; hypotype of Davis, 1887, pl. 138, fig. 6; M.C.Z. 7597. *4*, counter view of more rapidly expanding individual; hypotype of Davis, 1887, pl. 133, fig. 35; M.C.Z. 7596. *5–6*, counter and lateral views of form β individual; hypotype of Davis, 1887, pl. 133, fig. 34; M.C.Z. 7597. *7–15*, specimens numbered M.C.Z. 7592: *7*, calice of mature individual, cardinal fossula and cardinal and counter septa are clearly seen; *8*, transverse polished section of neanic portion of individual seen in *7; 9*, transverse polished section taken just below the calice of an adult individual, note fossula and axial depression; *10*, longitudinal polished section showing stereozones; *11*, transverse thin-section (×1½) taken below section illustrated in Fig. *9; 12*, front-calice view of early neanic individual showing pinnate septal insertion; *13*, lateral view of specimen in Fig. *12; 14–15*, counter and lateral views of late neanic individual. *16*, transverse thin-section of ephebic portion of form β individual (×1½); M.C.Z. 8975.

17–25—H. linneyi (Davis). *17–19*, counter, lateral and calice views; syntype of Davis, 1887, pl. 133, fig. 29; M.C.Z. 7609. *20–21*, counter and lateral views; syntype of Davis, 1887, pl. 133, fig. 28; M.C.Z. 7608. *22–23*, transverse thin-section of mature region of corallite (×2), and calice of same specimen; M.C.Z. 7612. *24–25*, counter and lateral views of good example of form β specimen; syntype of Davis, 1887, pl. 133, fig. 30; M.C.Z. 7610.

26–27—H. reynoldsi (Davis). Counter and lateral views; syntype of Davis, 1887, pl. 133, fig. 26; M.C.Z. 7626.

PART 1. COMPRESSION AND DEPRESSION IN SOME ONONDAGAN CORALS

INTRODUCTION

External shape of corals.—Only limited study has been made of the significance of flattened coralla, elliptical or sub-elliptical in transverse section, that occur sporadically in lineages of normally conical rugose corals. The remarkably flat-sided *Calceola* is generally familiar and corals with elliptical or nearly square cross-sections have been described.

Grove (1935) proposed the term "calceoloid" for horn corals flattened on either the cardinal or counter side. As the cardinal-counter plane is the plane of bilateral symmetry in the rugose corals the term "depressed," common in zoology, is more generally applicable to any coral with a non-circular transverse section in which the short diameter is in the cardinal-counter plane. If the short diameter is perpendicular to the cardinal-counter plane, the analogous term "compressed" applies. Easton (1951) coined the term "cuneate" for compressed rugose corals. Three possible deviations from the circular cross-section are thus defined, compressed (=cuneate), depressed, and a special case of the latter, calceoloid.

Zaphrentoid corals.—Hill, (1938, p. 23) defined "zaphrentoid" corals as "primitive" rugose corals with the following characteristics: solitary, pinnate septal plan, prominent fossulae, major septa extending to the axis, minor septa very short, complete tabulae, no dissepiments, and with considerable skeletal dilation in some forms. She listed 5 morphological groups (op. cit., p. 24–25) of such zaphrentoids, each composed of genera which "may form a related series, or be homeomorphs" (op. cit., p.23). Stumm (1949, p. 11) reviewed Hill's groups and added a sixth, and pointed out that 2 are typical of the Devonian and form the families Metriophyllidae and Zaphrentidae. The former is characterized by the presence of an axial deposit and stereoplasmic thickening of septa (Stumm, p. 6), the latter by the lack of any axial structure.

Certain parallels within the 6 groups are striking: *Zaphrentis* and *Heterophrentis* of the Zaphrentidae are with and without septal carinae respectively as are *Metriophyllum* and *Stereolasma* of the Metriophyllidae; in addition at least one other group may include septally carinate and non-carinate forms (Simpson, 1900, p. 203). Calceoloid (depressed) forms are known in at least 3 of the groups and cuneate (compressed) forms in at least 2. These and other homeomorphic features in the zaphrentoids make classification and recognition of evolutionary trends difficult. The present study is an attempt to clarify some details with regard to the depression and compression tendencies.

Devonian genera.—The genus *Homalophyllum* Simpson, 1900 (p. 221) was established for zaphrentid species which are flattened on the side of greatest longitudinal curvature. *Zaphrentis ungula* Rominger, 1876, was named as type species and *Zaphrentis herzeri* Hall, 1882, was cited as another example. According to Simpson (loc. cit.) "They make a natural group which differs from *Zaphrentis* and should be removed from that genus." Stumm (1949, p. 13) redefined the genus indicating its essential similarity to *Heterophrentis* except for its calceoloid flattening. Stumm gave *Heliophyllum exiguum* Billings, 1860, as another example.

As far as can be determined from the literature, little is known of the internal structure of the three species referred to *Homalophyllum*, or of other "zaphrentoid" corals which exhibit calceoloid flattening and which presumably might be referred to the genus. The need for such work is amply indicated by the present study which shows that the type species and at least one of the "examples" of *Homalophyllum* belong to the Metriophyllidae rather than the Zaphrentidae. Calceoloid flattening is certainly significant, but may occur in widely divergent stocks of the rugose corals.

This study is limited to corals of Onondagan age in eastern North America which exhibit the calceoloid and cuneate tendencies, but it is likely that some such species have been overlooked amongst the multitude of rugose corals that have been described. Other homeomorphic forms are discussed but were not studied in detail.

SYSTEMATIC IMPORTANCE OF CORALLUM FORM

The significance of the calceoloid and cuneate shape has been variously interpreted. *Homalophyllum* Simpson (1900) was established to include calceoloid species formerly assigned to *Zaphrentis*. Generic relationships are now interpreted differently but the definitive character of the genus is still calceoloid flattening. Similarly, *Compressiphyllum* Stumm, 1949, was defined on its peculiar cuneate form.

Easton (1951) made different interpretations with Mississippian corals. Genera and subgenera were defined on the basis of characters such as septal insertion and development, and the presence or absence of dissepiments, axial structures, etc. Most Devonian rugose coral genera are similarly defined. Easton recognized 3 potential "species-groups" in each of his genera or subgenera; one with a conical shape, one calceoloid, and one cuneate. The second and third type of "species-groups" were described in only a few genera, but when known were invariably coupled with one of the first type.

Most of the described calceoloid or cuneate genera and "species-groups" include but one species. The "species-group" classification more clearly indicates the fundamental relationships of the species, but at the same time minimizes the importance of external form, which is so useful in recognizing the group. Such de-emphasis, however, is probably justified on purely biologic grounds.

In the Devonian species described in this paper, earlier usage is modified as little as possible, although the desirability of change is recognized. Three or more species are referable to *Homalophyllum*. These are closely allied and may well represent a single offshoot from the normal ceratoid *Stereolasma*. In view of the number of species involved, the taxum *Homalophyllum* is useful, but its relationship to *Stereolasma* is best indicated by its recognition as a subgenus.

The calceoloid and compressed taxa *Aemulophyllum* and *Compressiphyllum* each include only one species. To be consistent they too are here recognized as subgenera of *Metriophyllum* and *Heterophrentis* respectively.

The compressed individuals of *Kionelasma* Simpson, and *Acrophyllum* Thompson & Nicholson, pose different problems. The former was defined as possessing a spongy axial structure which projects above the floor of the calyx as a prominent boss. This feature may not be of generic significance, but possible revision should await the study of the character in other groups. Compression is slight in *K. mammiferum* and may be absent or represented only by an elliptical boss. Likewise, *Acrophyllum* is defined on more fundamental characters than shape, and compressed individuals of *A. oneidaense* cannot be separated from normally round ones. Although apparently nonadaptive in character, the cross sectional shape of the corallite is of less than specific importance in both genera.

SIGNIFICANCE OF CORALLUM FORM

Depression.—The most familiar of the rugose corals showing the calceoloid form is the Silurian-Devonian genus *Calceola* from which the tendency takes its name. This genus differs from any described in this paper in the perfection of its flattening, in the presence of an operculum, and in that it is the counter rather than the cardinal side that is flattened. It has often been suggested that the flattening of *Calceola* is related to the presence of the operculum, a straight hinge line being an aid to proper functioning (see Grove, 1935, p. 357, for summary of literature). Others have suggested that the flat side was a resting surface. None of the genera here considered are operculate or derived from operculate ancestors so the former explanation of calceoloid flattening is inapplicable. The second explanation, however, may be pertinent as suggested by Grove (op. cit., p. 358) for *Aemulophyllum exiguum*.

Wells (1937, p. 15–16) has reviewed arguments on the environmental significance of the curved-conical body form of rugose corals. He concluded that an upright position is the natural one and that curved forms originate through the tendency of leaning or toppled forms to grow away from the substrate. Individuals of *A. exiguum* are fairly stable while resting on their flat surface. In this position the plane of the calyx rim is, in the majority of specimens, inclined to

the horizontal at an angle of only 10–25°. It seems likely that this was the living position of these forms and that the calceoloid flattening in *A. exiguum* needs no other explanation.

Similar arguments, however, do not necessarily apply to the other calceoloid species described. Most of them will rest on their flattened side with more stability than the curved-conical individuals of other species, but none so rests with its calyx far enough from the substrate to suggest that this was the living position.

Other workers (e. g., Easton, 1951, p.385) have argued thst the curved-conical body form results from the tendency of the upward growing polyp to bend toward the source of food and oxygen. The more or less consistent relationship in small corals, between the side of greatest longitudinal curvature and the cardinal or counter septum can be explained by an inherent tendency for the larva to orient itself on fixation, with the growing polyp later bending toward the current as described by Easton (loc. cit.). But in this case, the calceoloid coralla would offer a slightly broader front to the currents and would tend to be less stable than the conical forms. Most of the specimens under study give no indication of adult attachment.

It is suggested that calceoloid flattening in *Homalophyllum* represents a definite genetic trend in a metriophyllid stock and was not a response to environmental conditions. *Calceola*, *Aemulophyllum* and *Homalophyllum* are homeomorphic, but their depressed forms differ in detail and were derived independently, possibly in different ways.

Other calceoloid corals are known in various Ordovician (Duncan, 1957) to Mississippian (at least) coral stocks. *Holophragma* Lindstrom is a late Ordovician-Silurian example which is more similar to *Homalophyllum* than is *Calceola*, in that the flattening is on the cardinal side. *Triplophyllites* (*Homalophyllites*) *calceolus* (White & Whitfield), 1862, is a Mississippian species with marked calceoloid form although closely related species are normal ceratoid in shape. Grove (1935, p. 354–358) redescribed and illustrated this species and compared it with some of the Devonian forms here discussed. *T.* (*H.*) *calceolus* belongs to a different group of zaphrentoids than the Metriophyllidae (Hill, 1938, p. 25; Easton, 1951, p. 398).

Compression.—The compressed shapes of *Compressiphyllum*, *Kionelasma mammiferum* and *Acrophyllum oneidaense* should not be confused with the depressed form of *Calceola* and its homeomorphs, for the plane of compression is perpendicular to the plane of depression. The advantages of compression are hard to understand and perhaps there were none. The tendency appears in 3 rugose coral families considered here, and several representatives of 2 Mississippian families have been discussed elsewhere (Easton, 1951). In addition, Ordovician and Silurian forms are known (Duncan, 1956, p. 226, and explanation of pl. 22) and an analogous shape is found in scleractinian corals also (e.g., *Flabellum*).

Compressiphyllum had an erect growth position in its early stages at least, as is shown by the presence of supporting talons near the apex. It is possible that compression in an erect coral would have the slight advantage of presenting a narrower front to food and oxygen bearing currents. The growth position of *K. mammiferum* and *A. oneidaense* is unknown, but there is no reason to believe that it differed in any way from other curved-conical forms and there is no apparent ecologic advantage to the slight compression especially when it is limited to the calical boss. In *Kionelasma* and *Acrophyllum*, and perhaps in *Compressiphyllum*, compression is apparently a nonadaptive trend.

Summary.—Silurian to Mississippian depressed (calceoloid) corals are unrelated homeomorphs referable to at least three families. *Aemulophyllum* can be partly explained in terms of environmental adaptation, but *Homalophyllum* and other forms are apparently nonadaptive. None of the Devonian species seem to have been very widespread or long lasting.

Compressed (cuneate) corals are known from at least 3 Devonian families. *Compressiphyllum* may be adaptive but others are apparently not. Easton (1951) has discussed similar developments in two Mississippian families. The Devonian cuneate corals seem to have met with little success

and are only locally distributed in time and space.

SYSTEMATIC DESCRIPTIONS

Order RUGOSA

Family METRIOPHYLLIDAE

Genus STEREOLASMA Simpson, 1900

Stereolasma SIMPSON, 1900, p. 205–206.
Stereoelasma SIMPSON. STUMM, 1949, p. 7–8.
Stereolasma SIMPSON. HILL, 1956, p. 257–258.

Diagnosis.—Small, conical or calceoloid solitary corals. Major septa extending to the axis where they join and with added stereoplasm form a dense axial deposit; minor septa short. All septa are dilated at the periphery to form a marginal stereozone. Cardinal fossula commonly developed in the ephebic stage. Tabulae are arched against stereocolumella. No carinae or dissepiments.

Two subgenera are recognized:

1. Subgenus STEREOLASMA Simpson, 1900

Type species.—By original designation *Streptelasma rectum* Hall, 1877, pl. 19, figs. 1–13.

Diagnosis.—*Stereolasma* with a circular transverse section.

2. Subgenus HOMALOPHYLLUM Simpson, 1900

Homalophyllum SIMPSON, 1900, p. 221. GROVE, 1935, p. 353. STUMM, 1949, p. 13.

Type species.—By original designation: *Zaphrentis ungula* Rominger, 1876, p. 151, pl. 53, lower half, 2 right hand specimens.

Horizon and locality.—Jeffersonville limestone, Falls of the Ohio, Kentucky-Indiana.

Diagnosis.—Calceoloid *Stereolasma*, flattened on the convex, cardinal side. Flattening is most pronounced in early growth stages but even in adult stage produces an elliptical calice.

STEREOLASMA (HOMALOPHYLLUM) UNGULUM (Rominger), 1876

Pl. 104, figs. 1–16

Zaphrentis ungula ROMINGER, 1876, p. 151, pl. 53, lower tier, 2 right hand specimens. HALL, 1883, p. 296, pl. 23, figs. 2–4. HALL, 1884, pl. 30, figs. 4–8. DAVIS, 1887, pl. 133, figs. 32–35; pl. 138, fig. 6.
Homalophyllum ungulum (Rominger). SIMPSON, 1900, p. 221. STUMM, 1949, p. 13, pl. 5, figs. 5–7.

External features.—Medium-sized to small, ceratoid to trochoid corals, often becoming cylindrical. Calice margin elliptical, maximum ratio of long and short diameters: 2:1, minimum: 9:7. Dimensions of mature specimens: diameter at distal margin of calice, 18×14 to 32×18 mm.; length of corallum, 28–55 mm. Epitheca marked by irregularly spaced growth constrictions which bend upwards at the cardinal and counter positions; finer transverse or longitudinal markings are not preserved.

Calice moderately deep; the septal margins are steeply inclined along the sides, gently so on the bottom. Major septa extend from the margin almost to the axis; number 40–54; a narrow trench is formed between their axial ends (pl. 104, fig. 7). Cardinal fossula on convex, flattened side; occupied by short cardinal septum the distal edge of which is seen at the bottom of the fossula extending to the axis like other major septa; axial ends of adjacent major septa bend and form U-shaped fossular wall. Counter septum prominent, thicker than other major septa and projecting upwards slightly at axial end. Minor septa alternate with major; they are almost equally developed at edge of the calice, but extend less than halfway to the axis.

Two neanic individuals show interesting deviations from the above (pl. 104, figs. 12–15). The septal arrangement is pinnate with newly inserted septa forming a V-arrangement on the calyx wall by rapid divergence from the primaries; new septa are introduced at approximately 2 mm. intervals in the smaller specimen. Ephebic individuals show no addition of major septa in their calices and the major septa are only slightly divergent on the calyx wall.

Two distinct formae can be recognized: Forma α is composed of ceratoid or trochoid (side or front view) individuals marked by continuous expansion; the counter septum tends to be prominent in the calyx. Forma β is composed of longer individuals that expand more rapidly in early stages and become cylindrical in the distal $\frac{2}{3}$ of the corallum, or even decrease in diameter in the last $\frac{1}{3}$ (gerontic?) (pl. 104, figs. 5,6); the counter septum is thicker than the other major septa but does not project in the calice in any of the specimens studied.

Internal features.—Transverse sections immediately below the calice (pl. 104, figs. 9,11) show the major septa extending almost to the axis but distinctly not meeting; the axial ½ of these septa are strongly dilated, forming with added stereoplasm a large dense axial deposit (pl. I, figs. 9,11). An area between the septal ends in the sections corresponds to the axial depression in the calice. A wide peripheral stereozone is formed by dilation of major and minor septa and the minor septa project just inside of this zone. The 2 stereozones are separated by a narrow, open zone in which the major septa are relatively thin. The cardinal fossula extends almost to the axis cutting through the axial deposit where adjacent major septa join to form a U-shaped fossular wall; other major septa are more of less radially arranged. The open zone can be seen in some lower sections but in many the entire lumen is filled with stereoplasm through which the septa can be traced only with difficulty. No carinae are present.

In longitudinal section the lumen is almost entirely filled with stereoplasm (pl. 104, fig. 10); the few tabulae are thickened with stereoplasm and rise steeply toward the axial structure. In some sections the tabulae seem to continue across the axial region and in such individuals it is possible that the axial zone between septal ends is occupied only by the much thickened tabulae. No dissepiments.

Remarks.—The above description is based on the hypotypes of Davis, 1887, and other specimens in the Davis collection (M.C.Z., Harvard), all from the Falls of the Ohio and localities near Louisville, Kentucky. Rominger's syntypes are from the former location and there is no doubt of the identity of Davis' and Rominger's material.

This species has been previously referred to *Zaphrentis* and the Zaphrentidae, apparently on the basis of external appearance. The excessive deposits of stereoplasm and the axial structure of this form suggest a close relationship to *Stereolasma* and the *Metriophyllidae.*

Horizon and locality.—Jeffersonville limestone, Falls of the Ohio and localities near Louisville, Ky.

Material.—The Davis collection, M.C.Z. Harvard: Hypotypes (Davis, 1887) M.C.Z. 7594,5,6 and 7; topotypes, M.C.Z. 7592 (14 specimens) and 7593 (20 specimens).

STEREOLASMA (HOMALOPHYLLUM) LINNEYI (Davis), 1887
Pl. 104, figs. 17–25

?Zaphrentis herzeri HALL, 1882 (1884), p. 439, pl. 30, figs. 9,10, advanced sheets published in 1882. HALL, 1883, p. 292, pl. 21, figs. 7–9.
Zaphrentis exigua (BILLINGS). ROMINGER, 1876, partim, pl. 53, lower tier, bottom row, middle 2 specimens.
Zaphrentis linneyi DAVIS, 1887, pl. 133, figs. 28–31, pl. 138, fig. 5.
non *Kionelasma herzeri* SIMPSON, 1900, p. 208, fig. 25.
?Homalophyllum herzeri (HALL). SIMPSON, 1900, p. 221.

External features.—Medium-sized to small ceratoid or subcylindrical corals; calceoloid flattening on lower half of convex side; upper part not really flattened but sufficiently depressed so that the calice is elliptical in outline; maximum ratio of long to short diameters 4:3, minimum 8:7. Dimensions of mature individuals as follows: diameter at distal margin of calice, 13×10 to 21×18 mm.; length, 28 to 51 mm. Epitheca marked by uniform, more or less regularly spaced growth constrictions; finer growth lines in intervening spaces; finer transverse or longitudinal markings not preserved.

Calice moderately deep; septal edges almost vertical along sides, gently sloping to axis in central half. Major septa extend to the axis and meet without apparent twisting; number 28–40. Cardinal fossula on convex, flattened side; the cardinal septum extends to the axis but its distal margin is well below the other major septa. Counter septum projects above other major septa in periaxial region. Minor septa only slightly lower than major septa at rim of calice and extend less than halfway to axis.

Two formae, analogous to those described for *H. ungulum* are recognized: Forma α is composed of ceratoid individuals 31 to 37 mm. in length, averaging 15 mm. in calice diameter, and generally marked by continuous expansion. Forma β is markedly more robust, (pl. 104, figs. 24,25). One individual is 51 mm. long and 21 mm. in greatest calice diameter; the specimen expands rapidly for half its length and then becomes subcylindrical. *H. linneyi* forma β is similar

to *H. ungulum* forma β in general size and shape, but differs in cross-sectional shape, and calyx and growth-line characters. Each is identical to the corresponding form α in these respects.

Internal features.—A transverse section just below the calice shows the major septa extending to the axis; the axial $\frac{1}{3}$ of these septa are dilated to form a dense axial deposit and a peripheral stereozone is formed by dilation of both major and minor septa; the minor septa project just inside of this zone; the 2 stereozones are separated by a narrow open zone in which the major septa are relatively thin. The cardinal fossula is marked in the section by a slight invagination in the axial deposit.

No completely satisfactory longitudinal section has been seen but the general structure is as described for *H. ungula*.

Remarks.—The description is based on the 4 syntypes and other specimens in the Davis collection (Harvard M.C.Z.). The syntypes were illustrated but have not been previously described.

This species is closely allied to *H. ungula* from which it differs in the following respects: (1) calceoloid flattening is limited to lower half of corallum so that calice is markedly less elliptical, and (2) major septa meet at the axis.

Zaphrentis herzeri Hall, 1882, from the same locality is almost certainly conspecific with *H. linneyi* and if so has priority. The species was described on the basis of external characters as a zaphrentid. Presumably this is a mistake as in the cases of *H. ungula* and *H. linneyi*, but until Hall's types can be studied Davis' name should be used. Simpson (1900) referred *Z. herzeri* Hall to both *Kionelasma* (p. 208, fig. 25) and *Homalophyllum* (p. 221). The reference to *Kionelasma* is apparently a misprint as the species is nowhere mentioned in the text, and the specimen illustrated is in no way similar to Hall's species.

Two of the specimens illustrated by Rominger, 1876, as *Zaphrentis exigua* are referable to *Z. linneyi*. The second specimen from the left, bottom row, lower photograph, plate 53, has been examined and compares in every external character to the syntypes of Davis. The third specimen from the left has not been seen but should almost certainly be referred to the same species. Both specimens are from the Jeffersonville limestone, Crab Orchard, Kentucky.

Horizon and locality.—Jeffersonville limestone, various localities near Louisville, Kentucky.

Material.—Davis' syntypes are M.C.Z. #7608, 7609, 7610, 7611; additional topotypes M.C.Z. #7612.

STEREOLASMA (HOMALOPHYLLUM) REYNOLDSI (Davis), 1887

Pl. 104, figs. 26,27.

Zaphrentis reynoldsi DAVIS, 1887, pl. 133, figs. 25–27.

External features.—Small, ceratoid to subcylindrical corals, with calceoloid flattening on convex side. Calice margin strongly elliptical; ratio of long and short diameters 3:2. Dimensions of 2 syntypes as follows: diameter at distal margin of calice, both 12×8 mm.; length 24 and 30 mm. Specimens badly worn, features of epitheca unknown.

Calice poorly preserved; moderately deep, margined by moderately inclined septal edges, with little change in inclination in the bottom of the calice. Major septa extend almost if not quite to the axis, number 31; fossula on convex, flattened side, contains short cardinal septum apparently as in *H. ungula* and *H. linneyi*. Minor septa poorly developed.

Remarks.—The description is based on Davis' 2 syntypes, illustrated but not previously described. The specimens are poorly preserved and may be conspecific with either *H. ungula*, which they resemble in their elliptical cross-section, or *H. linneyi*, which they resemble in their ceratoid-cylindrical form. In the combination of these characters and in the poor development of minor septa *H. reynoldsi* stands apart from either of these species and is probably valid.

Neither specimen is well enough preserved to be sectioned and the species must be referred with question to *Homalophyllum* until additional material can be found.

Horizon and locality.—Jeffersonville limestone, 3 miles east of Louisville, Ky.

Material.—Davis' syntypes are in the M.C.Z. (Harvard) numbered 7625 and 7626.

Genus METRIOPHYLLUM Milne-Edwards & Haime, 1850

Metriophyllum M.-E. & H., 1850, p. lxix. STUMM, 1949, p. 7. HILL, 1956, p. 257.

Generic description.—External and internal features like *Stereolasma* except for the presence of horizontal carinae. Two subgenera are recognized:

1. Subgenus METRIOPHYLLUM Milne-Edwards & Haime, 1850

Type species.—*M. bouchardi* M.-E. & H., 1850, p. 69.

Diagnosis.—Conical *Metriophyllum* with a circular transverse section.

2. Subgenus AEMULOPHYLLUM, n. subgen.

Type species.—*Heliophyllum exiguum* Billings, 1860, p. 261, text-figs. 9,10.

Horizon and locality.—Onondaga limestone, Port Colborne, Ontario.

Diagnosis.—Calceoloid *Metriophyllum*, flattened on the lower part of the convex, cardinal side.

METRIOPHYLLUM (AEMULOPHYLLUM) EXIGUUM (Billings), 1860
Pl. 105, figs. 1–16

Heliophyllum exiguum BILLINGS, 1860, p. 261, text-figs. 9,10. NICHOLSON, 1874a, p. 29, text-fig. 6.

Petraia logani NICHOLSON, 1874a, p. 30–31, pl.3, figs. 3, 3a–f. NICHOLSON, 1874b, (1875?), p. 143–146, not fig'd.

Zaphrentis exigua (BILLINGS). ROMINGER, 1876, partim, p. 150–151, pl. 53, lower tier, top and bottom specimens in left column, upper 2 specimens in next column.

Heliophyllum (Zaphrentis) exiguum (BILLINGS). HALL, 1877, pl. 32, figs. 1–4.

Heliophyllum exiguum BILLINGS, var. HALL, 1877, pl. 32, figs. 5–7.

Cyathophyllum exiguum (BILLINGS). DAVIS, 1887, pl. 133, figs. 18–22; not pl. 78, fig. 7. LAMBE, 1901, p. 150–151, not fig'd.

Heliophyllum exiguum BILLINGS. STEWART, 1938, p. 36, pl. 6, figs. 4–5.

Zaphrentis exiguum (BILLINGS). FENTON & FENTON, 1938, p. 228, not fig'd.

Homalophyllum exiguum (Billings). STUMM, 1949, p. 13 (note only), not fig'd.

External features.—Small, curved turbinate, often becoming subconical or subcylindrical; calceoloid flattening on convex side limited to lower part of elongate coralla; apical angle measured in plane of flattening ranges from 55–95°, mean 75–80°; diameter at calice margin 9–26 mm., average 14 mm; length of convex side 6–26 mm., length-diameter ratio varies with shape of corallite. Epitheca transversely marked by 3 to 8 growth constrictions; in addition well preserved individuals show finer transverse striae; longitudinal markings weak or absent except on worn surfaces. Central part of calice moderately deep, surrounded by a platform about half the radius in width, septal edges gently sloping to almost vertical along sides of depression, horizontal or gently rising toward the axis along floor, no tabulae are visable in calice even in well preserved specimens.

The rim of the calice in majority of individuals is reflexed, with the septal margins arched upwards at the inner edge of the calicular platform (pl. 105, figs. 1–9). Major septa extend from the margin to the axis where they meet and form an axial whorl; number 24–37, average 29. Deep fossula on convex, flattened side extends to axis; occupied by a short cardinal septum. Fossula bounded by 2 major septa which parallel each other to center of calice; next adjacent major septa pinnately arranged, gradually becoming radial as outer limits of cardinal quadrants are reached; radial in counter quadrants (pl. 105, figs. 1,2,9,12). Cardinal septum lags behind other major septa in growth; marginally short, forms ridge on inside of peripheral stereozone; upper edge depressed in periaxial region then rises axially to position almost equal to that of other major septa. Minor septa alternate with major, markedly shorter even at the distal end of the corallite; form ridges on the inner surface of the calicular platform. All septa are marked by crossbar carinae; which descend gently toward the exterior; weakly developed or apparently absent in only a few individuals.

Internal features.—The arrangement of septa in transverse sections just below the calice is the same as in the calice; major septa extend to the axis where they meet and with added stereoplasm form a dense axial pillar whose diameter averages about ⅓ the diameter of the corallite (pl. 105, figs. 13,14). A wide peripheral stereozone is formed by the dilation of both major and minor septa; the minor septa extend only a little beyond this stereozone and appear as

ridges on its inner surface. Major septa are attenuate between the axial deposit and the peripheral stereozone.

Cardinal fossula bounded by two parallel major septa to which are joined in pinnate arrangement the adjacent 2–4 major septa on either side; the arrangement gradually becomes radial as the counter quadrants are approached. Cardinal septum extends to the axial pillar and fuses with it; markedly more attenuate than the other septa, and thinnest midway between the stereozones. The diameter of the pillar is constant or even increases downwards so that transverse sections of the early neanic stage are virtually filled with stereoplasm through which individual septa can be traced with difficulty. 20 to 25 major septa appear in neanic sections 5 and 6 mm. in diameter.

Carinae apparently limited to the peripheral zone (pl. 105, fig. 14); these have been variously interpreted. Nicholson (1874*a*, p. 31) interpreted them as "a succession of arched *grooves* (sic) of considerable width, separated by somewhat tumid interspaces." This is actually a rather good description of the appearance of most silicified specimens. Calcified specimens and some silicified ones show the carinae to be thin, delicate ridges very similar to those of *Heliophyllum*.

In longitudinal sections the axial deposit and outer stereozones are the most prominent features (pl. 105, fig. 15); tabulae can be identified only in the intervening space and are few in number, thin, gently or steeply rising toward the axis, and apparently limited to the neanic stage. No dissepiments.

Remarks.—This species has been variously interpreted in the past but apparently only on external features. Billings' original reference to the genus *Heliophyllum* was based on form and the presence of carinae. Nicholson (1874*a*) recognized Billings' species but described *Petraia logani* (1874*a* and 1874*b*) because the majority of his specimens, while superficially like Billings', were not structurally compatible with the genus *Heliophyllum*. Nicholson's types have apparently been destroyed and are not available for study. Rominger (1876) recognized the lack of dissepiments and referred the species to *Zaphrentis*. Lambe (1901) considered dissepiments to be present and referred the species to *Cyathophyllum* in agreement with Davis (1887) who however did not defend his generic assignment. Stumm (1949) referred the species to *Homalophyllum* thereby indicating his agreement with previous *Zaphrentis references*.

Aemulophyllum exiguum has several characters which together separate it from all other described species. The general structure and development is typical of the family Metriophyllidae: the axial deposit, the development of the fossula, and the complete lack of dissepiments, all point to this relationship. Within this family, *A. exiguum* has all of the features of *Metriophyllum* but differs from all species of that genus by its calceoloid flattening. On this basis alone *Homalophyllum* is separated from *Stereolasma*, and a new subgenus is needed for similar relatives of *Metriophyllum*. *A. exiguum* and *Homalophyllum* form an excellent example of homeomorphy.

Davis (1887) apparently intended to describe a second variety of *A. exiguum* in addition to *A. exiguum* var *elongatum* (Davis) described below. The label of the specimen illustrated by Davis (his pl. 78, fig. 7) is apparently in Davis' handwriting and reads as follows: "*Cyathophyllum exiguum* [=*Heliophyllum exiguum* Billings] varietas *subconicum* Davis, Middle Devonian, James Hill, 1 m. N. of Utica, Clark Co., Ind., Ky. Foss. Corals Pl. 78, fig. 7 (error in Explanation of Plate—should be as above. Wm. J. Davis.)" (Harvard M.C.Z. 8210). A second specimen identical in all important respects has virtually the same label but was not illustrated (M.C.Z. 8212). The external appearance is remarkably like *A. exiguum* except for the much larger size, almost perfect conical turbinate form, and the complete lack of flattening. These specimens should probably be referred to a separate but closely related species. The interior of the second specimen is not preserved, and in all probability the illustrated specimen is no better. Davis' name *subconicum* has no standing and nothing further can be done until more and better material is discovered.

Horizon and location.—Onondaga limestone, Edgecliff member, *Amphigenia* and lower coral zones, western New York; Onondaga limestone eastern New York (probably

Edgecliff) and Ontario; Jeffersonville limestone, Kentucky-Indiana region; Columbus limestone, Ohio.

Material.—Holotype of Billings, 1860: C.N.M. 3224g; syntypes: C.N.M. 3224, 3224a–d,f,h,–k. Hypotype of Hall, 1877: N.Y.S.M. 6245. Hypotypes of Davis, 1887: M.C.Z. 8206–7, 8220–22. Additional material listed in part II.

METRIOPHYLLUM (AEMULOPHYLLUM) EXIGUUM var. ELONGATUM (Davis), 1887

Pl. 105, Figs. 17–19

Cyathophyllum exiguum var. *elongatum* DAVIS, 1887, pl. 133, figs. 23–24.

Description.—With all the internal characters of the species proper, but robust and markedly more elongate; diameter 13–18 mm., number of major septa in calyx 27–35, length 26–33 mm.

Discussion.—This variety is identical to *A. exiguum* in all its essential characters and is linked to the typical members of the species by intermediate individuals. However, the variety is apparently fairly common at the Indiana-Kentucky localities, while the intermediate types are rare. The variety is therefore considered valid (see formae discussion in Part II of this paper).

Remarks.—The description and analysis is based on the syntypes of Davis and additional material in the Davis collection.

Horizon and locality.—Davis' material is from the Jeffersonville limestone at the Falls of Ohio and near Louisville, Ky.

Material.—Syntypes: M.C.Z. 8208, 8209; 10 topotypes (Davis coll.): M.C.Z. 8225.

Genus KIONELASMA SIMPSON, 1900

Kionelasma SIMPSON, 1900, p. 207–209. STUMM, 1949, p. 8. HILL, 1956, p. 270.

Type species.—By original designation, *Streptelasma mammiferum* Hall, 1882, p.21; 1883, p. 278, pl. 16, figs. 2,3, pl. 21, figs. 1,2.

Horizon and locality.—Jeffersonville limestone, Falls of the Ohio.

Diagnosis.—Like *Stereolasma* "except that stereocolumella [axial structure] is more high[ly] developed and produces an axial boss, while that of *Stereolasma* becomes less well developed in later growth stages and never produces a boss" (Stumm, 1949, p. 8).

Remarks.—In the original description of the type species, Hall (1882, p. 21; 1883, p. 278; 1884, p. 425) suggested calceoloid flattening; "expanded on the anterior, flattened on the posterior side." Simpson (1900, p. 207) described the calice more accurately as "circular or elliptic." Stumm (loc. cit.) makes no mention of this feature.

Actually the elliptical examples which have been studied are not depressed (calceoloid) but compressed (cuneate) with a fossula at one end of the ellipse rather than on the convex side as is usual in the metriophyllids. Specimens with a circular cross-section have been studied also and there is no basis for separating the compressed forms from the circular ones. If separated, however, the compressed form would have to be the type species.

KIONELASMA MAMMIFERUM (Hall) 1882

Pl. 105, figs. 20–26

Streptelasma mammiferum HALL, 1882, p. 21. HALL, 1883, p. 278, pl. 16, figs. 2,3; pl. 21, figs. 1,2. HALL, 1884, p. 425, pl. 24, figs. 12,13.

Kionelasma mammiferum (HALL). SIMPSON, 1900, p. 207–209, figs. 23,24. STUMM, 1949, p. 8, pl. 3, figs. 20–22.

The following description is based primarily on 2 compressed specimens, one of which, the original of Hall, 1883, pl. 16, fig. 2, is here designated lectotype, The description is supplementary to previous descriptions of the species and is only intended to indicate its position within the group of compressed and depressed forms under consideration.

External features.—Medium sized, curved trochoid corals, often with elliptical cross-sections which are more pronounced in mature portion of corallum; long to short diameters at base of calice as 3:2. Calice moderately deep, septal margins steeply inclined along sides, depressed periaxially, axially elevated to form prominent elliptic boss whose long axis parallels the long diameter of the calice. Major septa number 70–74, extend to the axis and are twisted together. Fossula deep but only in periaxial region; cannot be recognized on calicular margin and does not invade area of boss; may be located at either end of long diameter of calice (pl. 105, figs. 20,23). Differs from most other corals here described in that the plane of curvature of the corallum is perpendicu-

lar to the cardinal-counter plane. The fossula is not, therefore, located on the convex or concave side but at either "end" of the calice.

Internal features.—In transverse sections the major septa extend from the margin toward the axis where they become dilated and lost in stereoplasmic deposits forming the large axial structure which occupies approximately the axial ⅓ of the section. Minor septa extend ⅓ the distance to the axis. Peripheral stereozone formed by dilation of major and minor septa. Open zone between stereozones occupied by only slightly thickened major septa, the axial ⅓ of each minor septum, and by intercepted edges of tabulae (pl. 105, fig. 24). Fossula marked in section not far below the calyx by cardinal septum thicker than the other major septa but extending only part way to the axial structure; adjacent major septa are successively longer, the third on either side finally reaching the central area; these adjacent septa bend toward the fossula and form a series of U's which gradually become lost in the axial stereoplasm.

In longitudinal section the axial pillar is very irregular in outline; the peripheral stereozone and open zones have the same relative widths as in the transverse section, and both continue to the basal part of the corallum. Tabulae are more numerous than in any of the previously described species, irregularly spaced; arched against the stereocolumella. No dissepiments.

Remarks.—Neither Hall nor Simpson mention the fossula in their description of this species and genus, and Stumm (1949, p. 8) states "fossula obscure or lacking" in his generic description.

The fossula is, however, clearly marked in the calices of the specimens studied and in the transverse section of the lectotype. Simpson's illustration (1900, p. 208, fig. 23) is adequate to show the features he describes but differs in some details from the thin-section from which the sketch was made. Simpson's thin section (N.Y.S.M. #286) shows the fossula with adjacent major septa forming a U-shape around it as described above (pl. 105, fig. 26) . This is still more clearly shown on the polished base of the upper half of the corallum from which the section was cut (the section was taken about ¼" below the calice floor). In the calice of the same specimen the fossula is deep and limited to the periaxial region, also as described above. Interestingly enough, although this calice is round, the boss is strongly elliptical (pl. 105, fig. 25). The long axis of the boss would, if extended pass through the cardinal fossula; this axis is perpendicular to the plane in which the corallum is curved so that this round specimen shows the same tendency to being compressed as do the elliptical forms. This compression must be considered characteristic of the species and possibly of the genus.

Horizon and locality.—Jeffersonville limestone, Falls of the Ohio.

Material.—Lectotype (Hall, 1883, pl. 16, fig. 2), N.Y.S.M. 11057;hypotypes (Simpson, 1900, p. 208, fig. 23,24), N.Y.S.M. 286 and 287. Additional compressed specimen, N.Y.S.M. 11056.

Family ZAPHRENTIDAE
Genus HETEROPHRENTIS
Billings, 1875

Heterophrentis BILLINGS, 1875, p. 235. STUMM, 1949, p. 11–12. HILL, 1956, p. 270.

Diagnosis.—"Simple, ceratoid to trochoid corals. . . . A prominent cardinal fossula present along convex side of corallum. Septa of two orders, major and minor, of which former extend almost to axis and latter are very short. . . . Tabulae are complete or incomplete, extending all the way across corallum, and are horizontal in axial region, distally arched in the periaxial region, and bent abruptly downward as they approach the periphery. . . ." (Stumm, 1949, p. 12).

Two subgenera are recognized:

1. Subgenus HETEROPHRENTIS
Billings, 1875

Type species.—By subsequent designation *Zaphrentis prolifica* Billings, 1858, p. 176.

Diagnosis.—*Heterophrentis* with a circular transverse section.

2. Subgenus COMPRESSIPHYLLUM
Stumm, 1949

Compressiphyllum STUMM, 1949, p. 13. HILL, 1956, p. 270.

Type species.—By original designation, *Zaphrentis compressa* Rominger, 1876, p.151–152, pl. 53, lower tier, upper second figure from the right hand side (not *Z. compressa* Edwards and Haime 1860, p. 342). Romin-

ger's species was renamed *Z. davisana* by S. A. Miller, 1889.

Horizon and locality.—Jeffersonville limestone, Falls of the Ohio, Indiana-Kentucky.

Diagnosis.—*Heterophrentis* with pronounced compression along line perpendicular to cardinal-counter plane.

Discussion.—*Compressiphyllum, Kionelasma mammiferum, Acrophyllum oneidaense,* and several Mississippian species (Easton, 1951) are homeomorphic in their common cuneate form. This feature is so well developed in *Compressiphyllum* as to be considered a subgeneric character, whereas in the other species mentioned it is considered to be of specific or subspecific value.

HETEROPHRENTIS (COMPRESSIPHYLLUM) DAVISANA (S. A. Miller), 1889
Pl. 106, figs. 1–9

non *Zaphrentis compressa* EDWARDS, 1860, p. 342.
Zaphrentis compressa ROMINGER, 1876, p. 151, 152, pl. 53, lower tier, upper second figure from right. HALL, 1883, p. 295–296, pl. 21, figs. 4,5; pl. 22, fig. 5. HALL, 1884, pl. 30, figs. 1–3. DAVIS, 1887, fig. 3; pl. 138, fig. 4.
Zaphrentis davisana S. A. MILLER, 1889, p. 209. WERNER, 1932, p. 114–115.
Compressiphyllum davisana (S. A. MILLER). STUMM, 1949, p. 13, pl. 5, figs. 20–21.

External features.—Medium sized ceratoid (in cardinal or counter view) or trochoid (alar view) corals; alar sides are flattened parallel to cardinal-counter axis so that the long and short diameters are as 3:1; corallum gently curved in plane perpendicular to cardinal-counter plane. Calice deep, V-shaped in longitudinal section perpendicular to cardinal-counter plane; major septa extend to center where they are deflected in counter clockwise direction (from top); deep cardinal fossula at one end of oval contains a distally shortened cardinal septum; septa adjacent to fossula are deflect to form an oval depression that extends half the distance to the axial line.

Exterior marked by gentle growth constrictions which bend upwards on flat sides, fine longitudinal grooves mark the position of the septa. One specimen nearly 10 cm. long shows talons on apical 1 cm., indicating an erect growth position, at least in its early stages.

Dimensions of apparently average specimens: length, 80–100 mm; calyx diameter, 76×27 mm.

Internal features.—Transverse sections below the calyx show major septa extending almost or quite to a center line where most of them become mixed; cardinal septum extends to axial line and fossula is not well defined. Minor septa alternate with major, very short along sides, longer at cardinal and counter ends. A narrow peripheral stereozone is formed by dilation of septal ends; septa otherwise attenuate. No axial structure. Serial transverse sections from the same specimen show little change, except in number of septa from a diameter of 46×20 to one of 10×8 mm. (pl. 106, figs.1–8).

In longitudinal section the corallum interior is open except for the narrow peripheral stereozone and the tabulae. Tabulae wide spaced, periaxially arched, depressed axially and peripherally. No dissepiments.

Remarks.—This species is a typical zaphrentid and is like *Heterophrentis* s.s. in all essential details except for the compression. It is homeomorphic with *Kionelasma mammiferum* in which the relationship of the cardinal-counter plane, to the plane of curvature and compression are identical. The two species evolved independently and in *C. davisana* compression was much more pronounced than in *K. mammiferum.*

Horizon and locality.—Jeffersonville limestone, Falls of the Ohio.

Material.—Topotypes from the Davis collection, Harvard M.C.Z. #8976.

Family ACROPHYLLIDAE
Genus ACROPHYLLUM Thomson & Nicholson, 1876

Acrophyllum THOMPSON & NICHOLSON, 1876, p. 455. LAMBE, 1901, p. 174–175. STUMM, 1949, p. 14. HILL, 1956, p. 272.

Type species.—*Clisophyllum oneidaense* Billings, 1859, p. 128–129, not illus.

Horizon and locality.—Onondaga limestone, Rama's farm, and many places in the County of Haldimand, Ontario.

Diagnosis.—Simple ceratoid to subcylindrical corals; calyx with prominent axial boss formed by arching of the tabulae. Major septa are long, minor septa may be very short. Tabularium wide, formed by

strongly arched tabulae; peripheral dissepmentarium very narrow.

ACROPHYLLUM ONEIDAENSE (Billings), 1859
Pl. 106, figs. 10–17

Clisophyllum Oneidaensie (sic.) BILLINGS, 1859, p. 128–129, not illus.
Acrophyllum oneidaense (BILLINGS). THOMSON & NICHOLSON, 1876, p. 455.
Clisophyllum oneidaense BILLINGS. ROMINGER, 1876, p. 110–111, pl. 40, upper tier. NICHOLSON, 1874*a*, p. 20–21, pl. 4, figs. 4,5.
Acrophyllum oneidaense (BILLINGS). HALL, 1883, p. 301–302, text-figs. 1–2. DAVIS, 1887, pl. 94, figs. 1–2.
Clisophyllum oneidaense BILLINGS. SIMPSON, 1900, p. 212, fig. 32.
Acrophyllum Oneidaense (BILLINGS). LAMBE, 1901, p. 175–176, pl. 16, figs. 1,2.
?Acrophyllum rugosum GREENE, 1901, p. 48, pl. 17, figs. 1–3.
Acrophyllum oneidaense (BILLINGS). STUMM, 1949, p. 14, pl. 6, figs. 1–5. STUMM, 1951, card 37.

The following description is based on the only compressed specimen of this species available to the author and is supplementary to previous descriptions based on conical or cylindrical forms.

External features.—Medium sized, ceratoid or trochoid coral with compressed form decidedly more pronounced in mature portion of corallum. Dimensions as follows: diameter at distal margin of calice, 26×44 mm.; length, 70 mm. Epitheca marked by irregularly spaced growth constrictions which bend gently upwards at the approximate positions of the alar septa; fine longitudinal septal grooves correspond in position to the septa, those marking the minor septa being only faintly developed. The proximal ⅔ of the epitheca is marked by numerous elliptical nodes which seem to be arranged in transverse rows; individual nodes project a distance approximately equal to their diameters; they are evidently not spine or rootlet bases and function if any is unknown.

Calice elliptical, moderately deep; septal margins steeply inclined along sides, almost horizontal in periaxial region; a few septa are axially elevated without twisting to form ridges on prominent elliptic boss the long axis of which parallels the long axis of the calice. Cardinal fossula occupied by aborted cardinal septum; deep, extends from margin of calice to boss; located at end of ellipse on convex side of mature portion of corallum; early neanic curvature is in a plane perpendicular to the cardinal-counter plane but appears to be due to an accident.

Major septa number 86; alar septa and 2 or 3 others extend to axis where they meet in pairs and form prominent ridges on boss; other major septa stop at the margin of the boss. Septa pinnately arranged in cardinal quadrants which occupy approximately ⅓ of the calice; radially arranged counter quadrants contain nearly twice as many septa. Major septa were introduced on either side of the cardinal septum and on the counter side of the alar septa; late introductions in these four positions are the only short septa that are visible in the calice. Minor septa not seen in calice, but a broken exterior shows rudimentary minor septa to be developed on the inner surface of the epitheca. Their presence is further indicated by the existence of septal grooves corresponding to major septa and to the position of minor septa.

Internal features.—In a transverse section just below the calice the major septa are attenuate and extend to the boss where the majority stop; about 6, however, extend irregularly to the axis where they fuse in pairs. Intercepted edges of tabulae form very fine, fairly numerous, concentric lines. Structure of narrow peripheral dissepimentarium is indistinct and minor septa are not visible. Cardinal and alar fossulae are clearly marked and short septa can be seen only in these positions. Lower transverse sections are similar except that septa are relatively thicker, leaving less interseptal space.

A longitudinal section of the proximal half of the corallum shows the very wide tabularium occupied by steeply arched complete and incomplete tabulae; structure of narrow, peripheral dissepimentarum is obscure.

The upper half of the corallum has not been sectioned but decorticated areas show clearly the presence of rudimentary minor septa and a narrow peripheral zone of steeply inclined dissepiments.

Remarks.—The rudimentary minor septa are mentioned by Rominger (1876), Hall (1883), and Lambe (1901), whereas Stumm (1949, p. 14) considered that the minor septa extended to the boss. This latter is ap-

parently a misinterpretation due to the very poor development of these septa which are not visible on all specimens.

The nodes have been noted by the above three authors on material from Ontario and the Falls of the Ohio. Apparently the nodes vary in form and extent and may be absent in some specimens.

It seems likely that *Acrophyllum rugosum* Greene, 1901, is synonymous with *A. oneidaense*, although positive determination of this would involve study of numerous examples in addition to the types. Greene's species is inadequately described and illustrated but external features, including the nodes, seem identical. Stumm (1951) suggested that Ontario (type area) and Falls of the Ohio specimens of *A. oneidaense* may not be conspecific. This seems unlikely in view of the present study, but if so the material of Rominger (1876; in part), Hall (1883), Davis (1887) and the present author, would possibly be referred to Greene's species.

Compression in this species is mentioned by Hall (1883), p. 301) but according to him "this may have resulted from accident." Greene (1901, p. 48) indicates that "small compressed examples" of *A. rugosum* (=*oneidaense?*) are fairly common. It is noteworthy that all known compressed examples of the species are from the Falls of the Ohio; none have been recorded from Ontario.

TABLE 1—SPECIES WITH NON-CIRCULAR CALICES DESCRIBED BY JAMES HALL

Species	Hall, 1884			Hall, 1883			Loc.*	Hall (1884) quotation
	Page	Pl.	Fig.	Page	Pl.	Fig.		
1. *Streptelasma mammiferum*	425	24	12, 13	278	16 21	2–3 1–2	J	"flattened on posterior side"
2. *S. coarctatum*	425	24	16, 17	275	15	15, 16	J	"usually slightly compressed"
3. *Zaphrentis complanata*	430	28	1				O	"compressed"
4. *Z. subcompressa*	432	28	7, 8	286	18	8, 9	J	"somewhat flattened"
5. *Z. colletti*	432	29	5, 6	315	18	12, 13	J	"usually compressed"
6. *Z. fusiformis*	433	29	1, 2	296	21	12, 13	J	"a little compressed"
7. *Z. ovalis*	433			294	23	1	J	"slightly compressed"
8. *Z. fastigata*	434						O	"usually compressed"
9. *Z. trisutura*	434			289	20	1–3	J	"quadrilateral"
10. *Z. herzeri*	439	30	9, 10	292	21	7–9	J	"frequently . . . the anterior side is flattened"
11. *Z. elegans*	441			287	19	2–5	J	"usually slightly compressed"
12. *Z. convoluta*	441			294	22	2	J	"slightly compressed"
13. *Cyathophyllum scalenum*	446						J	"compressed"
14. *Heliophyllum annulatum*	452			307	23 25	12 2–3	O, J	"usually compressed"
15. *H. latericrescens*	453			314	27	1	J	"slightly compressed"
16. *H. lineolatum*	454						J	"compressed . . . may be due to accident"

* Horizon and locality: O, Onondaga ls, New York; J, Jeffersonville ls, Indiana-Kentucky.

The described specimen has all of the characters of the species, differing only in its strongly compressed shape. In body form the specimen is homeomorphic with examples of *Kionelasma mammiferum* and *Compressiphyllum* previously described although these differ in fundamental skeletal details and are assigned to different families. *A. oneidaense* differs from the other two in relationship of the plane of curvature to the cardinal-counter plane. In all of the other corals described, and in *A. oneidaense* the curvature is in this plane and the cardinal fossula is on the convex side. In *K. mammiferum* and *Compressiphyllum* the plane of curvature is perpendicular to the cardinal-counter plane and the fossula is in a left- or right-hand position.

Horizon and location.—Jeffersonville limestone, Falls of the Ohio, Indiana-Kentucky.

Material.—The specimen described is in the New York State Museum where it is numbered 11054.

SYSTEMATIC ADDENDA

Table 1 lists a number of species described by Hall in 1882 and illustrated by him in 1883 and 1884. In each case Hall suggested a non-circular cross-section in the quoted terms. Species 1 and 10 have been discussed in this paper but the others are only listed because the nature of their shape and the systematic positions of the species are unknown. Many are only slightly non-circular. Some are probably synonymous with species which have been considered, and others are perhaps accidentially deformed. All must be restudied before any conclusions can be drawn.

In most cases (nos. 5,7,11,12,14,16) Hall's illustrations are inadequate to indicate corallum shape. Two others have never been illustrated (13,15). Some are shown by illustration to be elliptical in cross-section, but the orientation relative to the cardinal-counter plane is unknown (nos. 6,9, and questionably 2 and 4). The type specimens of two have been examined: one, the holotype of *Z. complanata* (no. 3, table 1) is too badly crushed and broken for determination; the other, the holotype of *Z. fastigata* (no. 8, table 1) is slightly compressed but its systematic position is unknown.

These additional "species" are of interest in indicating that compressed and depressed coralla are perhaps more common than is indicated in the literature.

PART 2. INDIVIDUAL VARIATION IN *METRIOPHYLLUM* (*AEMULOPHYLLUM*) *EXIGUUM* (BILLINGS) 1860

INTRODUCTION

During the summmer of 1956 the author collected some 250 specimens of *Aemulophyllum exiguum* which had weathered free of an outcrop of the Edgecliff biostrome member of the Onondaga limestone, near Clifton Springs, New York. Extreme variation in this collection suggested a study of individual variation in a single population or community. Additional material, including Billings' syntypes and the hypotypes of various authors were borrowed and much of the systematic description of Part I was based on such specimens. The discussion of variation, however, is based almost entirely on the Clifton Springs collection, although comparison is made with the other material.

MATERIAL STUDIED

The following is a catalog of the localities and specimens of *A. exiguum* involved in this study.

Collected by the author.—Locality 445: 1 mile N.E. of Clifton Springs in the Phelps (7½ and 15 min.) quadrangle, New York. Edgecliff biostrome member (Zone C), Onondaga limestone. 254 silicified individuals weathered free of matrix, 7 calcareous individuals; other individuals in matrix were collected and some were later freed by solution in acid. This group of fossils is the main basis for the study of individual variation in the species.

Locality 113: Road cut, N.E. corner of Lancaster (7½ min.) quadrangle, N.Y. Zone B (*Amphigenia* zone), Edgecliff member, Onondaga limestone. 10 to 20 silicified individuals freed from matrix with acid, generally poorly preserved.

Locality 380: Abandoned quarry, 2 miles E.N.E. of Williamsville (Lancaster, 7½ min.

quad), N.Y., Zone B ((*Amphigenia* zone), Edgecliff member, Onondaga limestone. Three silicified, well preserved individuals.

New York State Museum.—No. 6245, hypotype of Hall, 1877, pl. 32, figs.1–3; silicified specimen from the Onondaga limestone, Clarence Hollow, Clarence 7½ min. quadrangle, New York.

Three additional calcareous specimens made excellent sections. One of these is labeled Williamsville (Lancaster quad.) and two Schoharie (Schoharie quad.), N.Y. All are from the Onondaga limestone.

Canadian National Museum.—No 3424g, labeled holotype, and 3424, a–d, f, h–k, labeled syntypes, all of Billings, 1860. No. 3424g appears to be the specimen illustrated by Billings. The specimens are from the Onondaga limestone, Rama's Farm, Port Colborne, Ontario. They are silicified and poor material for sectioning.

Museum of Comparative Zoology, Harvard University—No's. 8206–7, 8220–22, hypotypes of Davis, 1887; No's. 8224 (15 specimens) and 9058 (8 specimens) all from the Falls of the Ohio and various localities in the vicinity of Louisville, Ky., No's. 8208, 9 hypotypes of Davis, 1887, and No. 8225 (5 specimens), all of *A. exiguum* var. *elongatum* (Davis) 1887, from the same localities. Most of the specimens in the Davis collection are silicified, but some are only partly so and are well preserved inside as well as out.

Museum of Paleontology, University of Michigan.—No. 8618, 6 hypotypes of Rominger, 1876; 4 specimens are referable to *A. exiguum;* one is referred to *H. linneyi* (Davis); and one cannot be referred to any species with certainty until it is sectioned.

PREVIOUS WORK

Comparatively little has been done on individual variation in rugose corals from a single horizon and locality. Wells (1938) paper on *Heliophyllum halli* Milne-Edwards and Haime is an exception, and he included a summary of sparse earlier work.

Hall (1877) recognized variations in *A. exiguum* and illustrated "*Heliophyllum exiguum* var." (pl. 32, figs. 5–7). Hall's plates were unaccompanied by text and his ideas are unknown. Fenton and Fenton (1938) provided a text for Hall's species of *Heliophyllum* and saw no reason to recognize the variety (op. cit. p. 228). Hall's form is connected to the typical form by intermediate types and cannot be considered a variety, but is recognized as Forma ϵ below.

Davis (1887) illustrated, but did not describe, "*Cyathophyllum exiguum* var *elonga-*

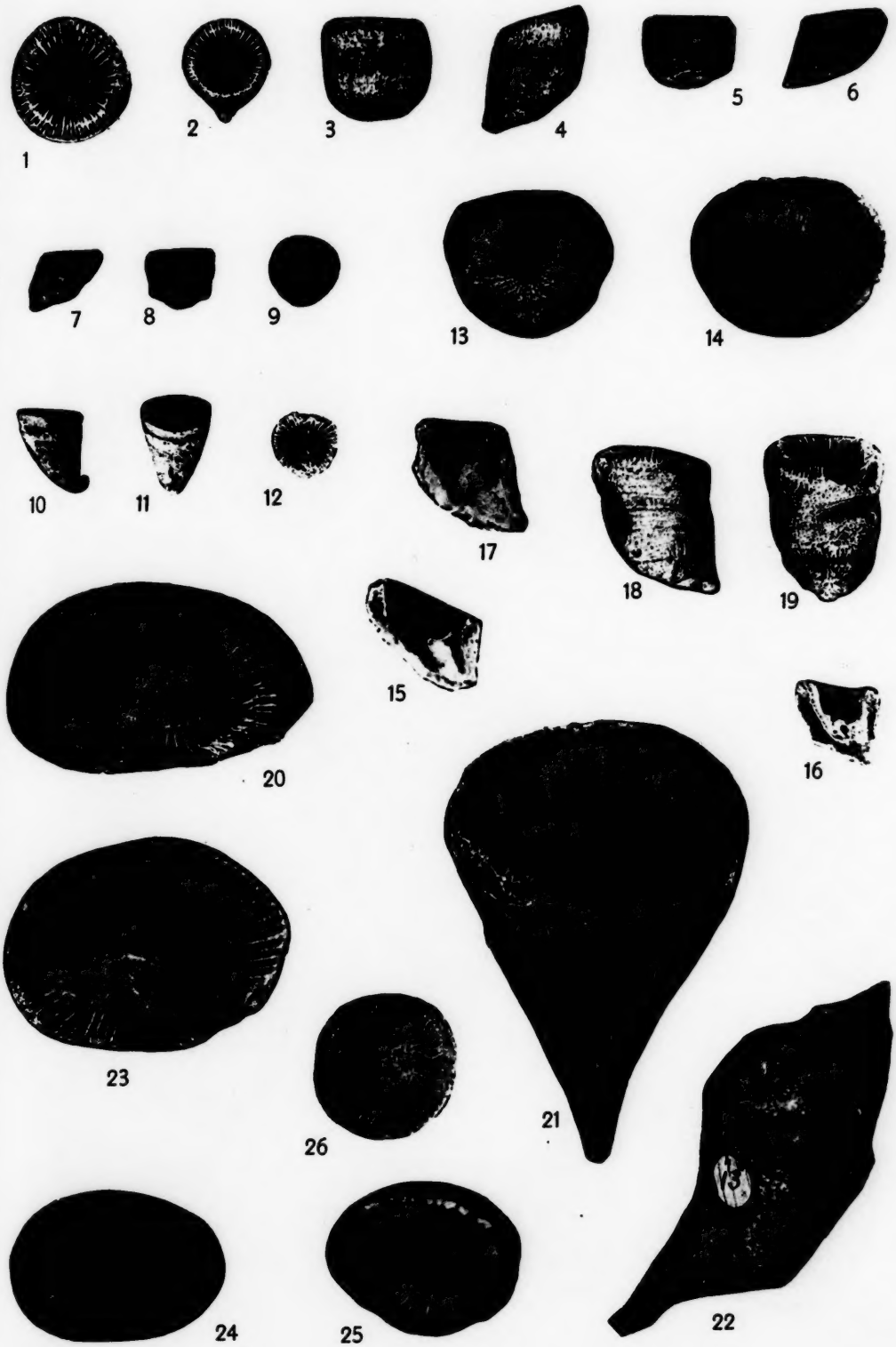
EXPLANATION OF PLATE 105

All figures ×1 unless otherwise indicated

FIGS. *1–16—Aemulophyllum exiguum* (Billings). *1–2*, calices of form β and ζ individuals respectively, both M.C.Z. 8224; *3–4*, cardinal and lateral exteriors of form γ specimen, M.C.Z. 9058; *5–6*, cardinal and lateral exteriors of form β specimen, M.C.Z. 8224; *7–9*, lateral, cardinal and calice views of form ϵ individual, syntype of Billings, 1860 (not illus.), G.S.C. 3424i; *10–12*, lateral, counter and calice views of form ζ individual, syntype of Billings, 1860 (not illus.) G.S.C. 3424j; *13*, transverse thin section (×1½) of adult portion of β individual showing stereozones, cardinal fossula and carinae, N.Y.S.M. 11055 (Schoharie, N.Y.); *14*, transverse thin section (×1½) of adult portion of β-ζ specimen showing same features as *13*, M.C.Z. 8224, *15*, longitudinal polished section of β specimen showing axial deposit and outer stereozone, M.C.Z. 8224; *16*, broken specimen (form β-γ) showing carinae and shape of calice, Loc. 445.

17–19—A. exiguum var. *elongatum* (Davis). *17*, longitudinal polished section showing stereozones, M.C.Z. 8225; *18–19*, lateral and counter views, syntype of Davis, 1887, pl. 133, fig. 23, M.C.Z. 8208.

20–26—Kionelasma mammiferum (Hall). *20–22*, calice, concave side and cardinal views respectively; cardinal fossula is on right hand side in first two figures and calical boss is elongated in cardinal-counter plane; N.Y.S.M. 11056. *23–24*, calice with cardinal fossula on left side (note elongate boss) and transverse polished section of underside of same specimen (so fossula appears on right side); the concave side is down in both pictures; syntype of Hall, 1882 (1883, pl. 16, fig. 2), here designated lectotype; N.Y.S.M. 11057. *25–26*, calice and transverse section of conical individual oriented with concave side down and cardinal fossula on right, note boss elongage in cardinal-counter plane; hypotype of Simpson, 1900, Fig. 23; N.Y.S.M. 286.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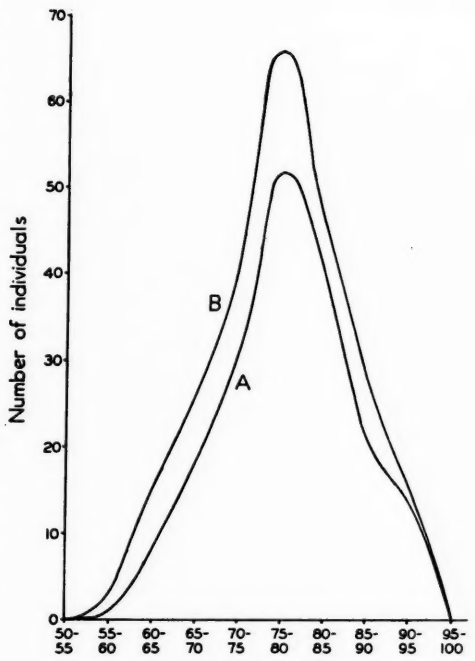
tum" (pl. 133, figs. 23–24). This variety is also connected to the typical form by intermediate individuals, but the intermediates are rare while the variety is apparently common at the Kentucky localities. For this reason the variety is considered valid but is designated as Forma δ to indicate its position in the variation scheme of *A. exiguum*.

INDIVIDUAL VARIATION IN *M.* (*AEMULOPHYLLUM*) *EXIGUUM* (BILLINGS)

The characters on which this analysis of variation is based are all external. Too few specimens are sufficiently well preserved for internal analysis, but some representatives of most of the formae have been studied internally and very little variation other than that related to external shape and size has been noted. The characters of the calice are stable, and limited variation in this feature is directly related to external shape, rate of expansion relative to length increase, and size. These last 3 form the basis for the study.

Rate of diameter increase relative to length can best be represented by apical angle, and the first step in this study was to divide all the individuals with well preserved apices into 5° classes, the angle being measured in a plane parallel to the plane of calceoloid flattening. The distribution of 186 such individuals from locality 445 is shown on the graph (text-fig. 1). The distribution is normal over a rather wide range (55–95°) with a single peak at 75–80°. A second curve on the same graph shows the apical angle distribution of 239 individuals, including all those studied (see list above) which are sufficiently well preserved for the measurement to be made.



TEXT-FIG. *1—Aemulophyllum exiguum.* Frequency distribution 5° classes of apical angle measured in plane of flattening. Curve A, 186 individuals from locality 445. Curve B, 239 individuals from New York (including loc. 445), Ontario and the Kentucky-Indiana localities.

Secondly, divisions were made within each apical angle class on the basis of form of the corallum: patellate, conical, cylindrical, and combinations. These are the basis for the formae described in the next section. Figure 2 shows the apical angle

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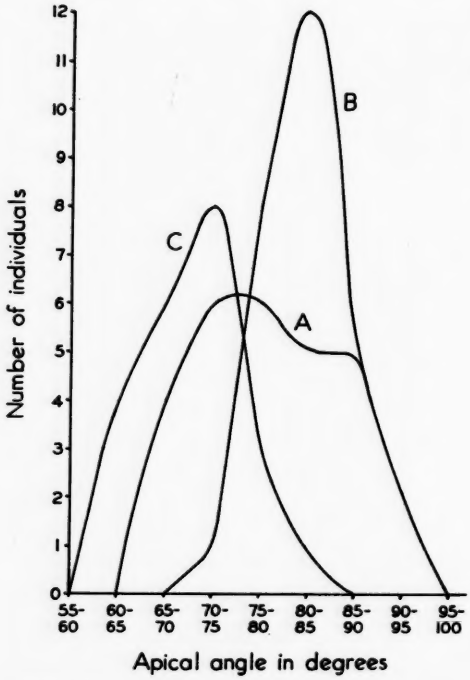
EXPLANATION OF PLATE 106

All figures ×1 unless otherwise indicated

FIGS. *1–9—Compressiphyllum davisana* (S. A. Miller). *1–8*, serial transverse sections (×1½) showing development of compression with growth; all sections are seen from above and are similarly oriented with cardinal septum at the top; sections cut from a single individual with calice dimensions of 26×75 mm., M.C.Z. 8976. *9*, longitudinal thin-section of another specimen, M.C.Z. 8976.

10–17—Acrophyllum oneidaense (Billings). All photographs are of same specimen (N.Y.S.M. 11054). *10–12*, counter, and 2 alar views of exterior. *13*, calice showing cardinal and slight alar fossulae and elongate boss. *14–16*, serial transverse polished sections in descending sequence; all oriented with cardinal fossula up but *14* and *16* reversed (left to right) relative to Figure *13;* note alar fossulae. *17*, portion of longitudinal polished section.



TEXT-FIG. *2—Aemulophyllum exiguum.* Frequency distribution in 5° classes of apical angle measured in plane of flattening. Curve A, 28 individuals of Forma α. Curve B, 28 individuals of Forma β. Curve C, 22 individuals for Forma ζ. All specimens are from locality 445.

distribution of 3 of the most common formae. Forma α has essentially the distribution of the species. The curve is based on 28 individuals from locality 445 and minor deviations are due to the smallness of the sample. Formae β and ζ show distributions quite different from that of the species. Both are derived from forma α and both go through an α stage, but the cylindrical β must have been derived from a rapidly expanding (wide angled) α, while the subconical ζ could only be derived from α's with smaller apical angles.

The third basis for this study of variation is the size of individuals. Size, however, is a function of apical angle, body form and age. Each of the lineages suggested below is characterized by increase in overall bulk, length and diameter.

The three factors combined, rate of diameter increase relative to length, shape of corallum, and size, when used together are sufficient to define the 6 formae described below.

ANALYTICAL KEY TO FORMAE

I. patellate corallum
  A. apical angle >80°..... α_1
  B. apical angle <80°..... α_2
II. elongate corallum
  A. corallum patellate becoming subcylindrical
    1. cylindrical stage <$\frac{1}{2}$ of length ... β
    2. cylindrical stage >$\frac{1}{2}$ of length
      a. stages sharply defined
        i. diameter >12 mm..... γ
        ii. diameter <12 mm..... ϵ
      b. large individuals, ill defined stages..... δ
  B. corallum subconical
    1. apical angle 70–85°, diameter >12 mm..... ζ_1
    2. apical angle 60–70°, diameter <12 mm..... ζ_2

DESCRIPTIONS OF FORMAE

Forma α (text-fig. 3*a*).—Patellate, subpyramidal, rate of expansion (in diameter) proportional to rate of increase in length; cardinal exterior very flat, triangular; length on counter side very short; apical angle 65–95° (text-fig. 2). Common at locality 445; also found at localities 113, 380 and in Ontario (C.N.M. #3424k) and Indiana-Kentucky (M.C.Z. #8224 and #9058).

Forma β (text-fig. 3*b*; pl. 105, figs. 1,5,6, 15).—Subpyramidal becoming subcylindrical, shape caused by marked slow-down in rate of expansion at a point about $\frac{1}{2}$ to $\frac{2}{3}$ the distance from the apex to the calyx rim measured on the cardinal side; cardinal exterior flattened for $\frac{1}{2}$ to $\frac{2}{3}$ the length, convex above; apical angle 70–95°, mean 80–85° (text-fig. 2); robust, diameter 10–17 mm., average 14 mm. Common at locality 445, and at the Indiana-Kentucky localities (M.C.Z. #8220, 8224), also found in Ontario (C.N.M. #3424c) and at other places in New York: Loc. 113, and N.Y.S.M. specimens from Schoharie and Clarence Hollow (N.Y.S.M. #6245, hypotype of Hall, 1877, Pl. 32, Figs. 1–3.)

Forma γ (text.Fig. 3*c*; pl. 105, figs. 3,4).—Like robust forms of β but the flat, subpyramidal portion is the lower $\frac{1}{3}$, the upper $\frac{2}{3}$ being cylindrical; diameter 14–18 mm.; apical angle 75–90°. This form is rare, only 4 examples being known, 2 from locality 445

and 2 from Indiana-Kentucky (M.C.Z. #9058).

Forma δ (text-Fig. 3*d*; pl. 105, figs. 17–19).—Like γ but decidedly larger, and more irregular in its characters; flattening and breaks in profile less pronounced. This is *Aemulophyllum exiguum* var *elongatum* (Davis) 1887, included here because of its apparent terminal position in the α-β-γ-δ lineage discussed below. Apparently rather common at the Indiana-Kentucky localities: M.C.Z. 8208 and 8309 (syntypes), and 8225 (10 specimens).

Forma ε (text-fig. 3*e*; pl. 105, Figs. 7–9).—Similar to γ but more delicate in appearance; apical angle 60–80°, mean 75–80°; diameter 9–12 mm. This form is to γ as ζ_2 is to ζ_1, but the complete gradation in size and apical angle from one to the other is lacking. Instead the 2 forms overlap in the rages of their apical angles but are quite distinct in size. Common at locality 445; in addition one Ontario specimen has been studied (C.N.M. #3424i), and the individual illustrated by Hall (1877, Pl. 32, Figs. 5–7) as "*Heliophyllum exiguum* var." from western New York belongs to ε. The present location to Hall's specimen is unknown.

Forma ζ (text-fig. 3*f*; pl. 105, figs. 2, 10–12).—Subconical due to gradual decrease in expansion rate, lower part of cardinal exterior shows flattening tendency; apical angle 60–85°, mean 70–75° (text-fig. 2). Maximum diameter varies with apical angle from 9–15 mm. On this basis 2 subformae can be recognized: ζ_1 is robust, apical angle 70–85°, diameter 12–15 mm.; ζ_2 is more delicate in appearance, apical angle 60–70°, diameter 9–12 mm. There is a greater tendency to calecoloid flattening in the more robust form (ζ_1). Common at locality 445; also found at locality 113. This is the most common form in the collection of syntypes (C.N.M. #3424a,g,h) all from Port Colbourne, Ontario, and is found in the Indiana-Kentucky collections (M.C.Z. #8224 and 9058).

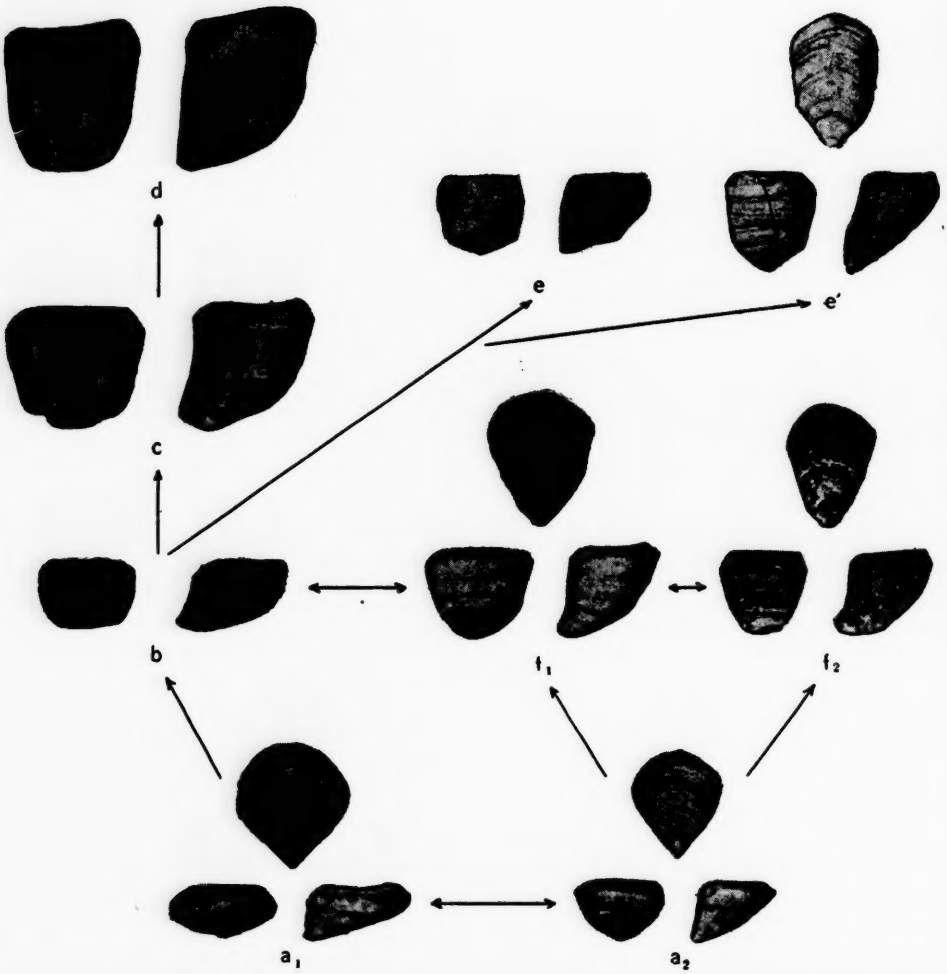
FORMAE RELATIONSHIPS

The interrelationships between the described formae are shown in figure 3. While form β would appear to be the normal or typical form of the species it is apparent that α must be considered the starting point. In all probability form α is composed in part of neanic individuals, but the extreme flattening of some individuals is unmatched in other formae and in addition many have the full diameter and calyx characteristics of the other forms; these must be considered fully developed. Variations within form α were random; the apical angle is a function of rate of increase in diameter (polyp growth) relative to increase in length. For a given rate of polyp growth a small apical angle represents more rapid deposition of skeletal material than does a wide apical angle, or conversely, for a given deposition rate a large apical angle represents more rapid polyp growth. Some forms expended their energy in rapid size increase; these are true members of $\alpha(\alpha_1)$. Others increased at a more moderate rate but were perhaps killed before being fully developed. These also are referred to $\alpha(\alpha_2)$. There is a complete gradation from small to large apical angles, from probable immature specimens to almost certain adults.

Whatever the nature of the form α specimens themselves, it is certain that the other, longer forms went through an α stage in their ontogeny. Both phylogenetically and ontogenetically two direct derivatives can be recognized. Form β represents a form α stage on which has been superimposed cylindrical growth, that is, length increase with only slight diameter increase. In some individuals a second stage of diameter increase separates a lower, brief cylindrical stage from the final stage. Form β individuals could develop only from wide angled, α_1 forms. Without the early rapid increase, true cylindrical growth could not be attained. There are all gradations between form α_1, and β and considerable variation in diameter within β as indicated previously.

Form ζ is a second direct derivative of form α. The initial stage can be termed an α_2 stage. With a smaller apical angle, diameter increase continued throughout the life of the individual. Some decrease in rate of increase is evident but no sudden change in growth took place, thus a subconical rather than a cylindrical form developed. There are all gradations between form α_2 and ζ.

As indicated in figure 3, β-ζ gradational



TEXT-FIG. 3—Formae of *Aemulophyllum exiguum* (Billings). Rising arrows indicate the apparent relationship between the formae; horizontal arrows indicate known continuous variations between formae. Views (×1) are posterior (cardinal side) and left lateral with the distal margin oriented horizontally in both. Posterior-ventral views of some forms are taken in plane of flattening to show apical angle. All specimens from locality 445 except c and d which are from the Indiana-Kentucky localities. Key: a = α, b = β, c = γ, d = δ, e = ϵ, f = ζ.

forms are known. This is to be expected from the α_1-α_2 gradation. The majority of individuals, however, are easily referable to one or another form. Variation within form ζ is interesting. Apical angle variations from 60–85° show a direct relationship to diameter variations from 9–15 mm. A study of 22 individuals from locality 445 shows that 10 range from 60–70° and 9–12 mm., while 12 range from 70–85° and 12–15 mm; these are considered subformae and designated ζ_2 and ζ_1, respectively.

Similar variation is noted in β derivatives, but division is made on a somewhat different basis. The majority of forms are comparatively short (β proper). Perhaps length increase was slow because of the large diameter, a given amount of skeletal material causing less length increase than in ζ. Variation in β is considerable: diameter

10–17 mm., apical angle 70–95°, but the relationships between these 2 variable are not so close that subforms can be recognized. Comparatively few individuals show the increase of length characteristic of ζ. Those that do however, are of 2 distinct types and are sufficiently set off from each other as to be recognized as different formae. Form ϵ is analogous to ζ_2 in that it is of smaller diameter. Its main characteristic however, is the pronounced development of the cylindrical stage. Form γ is distinctly more robust and was developed from a β-form of maximum diameter. It too is characterized by the length of its cylindrical stage. Forms ϵ and γ are sharply separated and related only through β.

Both ϵ and γ individuals are less numerous than β or ζ individuals. It seems likely that β and ζ forms utilized similar amounts of material in their skeletons, β being shorter, but stouter. Form ϵ, derived from small β forms, would utilize little more perhaps than large β forms but a smaller polyp did the work. The robust γ individuals would require much additional material and are the rarest of the lot.

From the above paragraphs it might be surmized that forms ϵ and γ are composed of gerontic β individuals. Possibly in some cases that is so; certainly both forms are joined to β by intermediate individuals. However, there are more ϵ individuals than intermediate ones. This should not be so if the relationship were purely ontogenetic. In addition, ϵ individuals have certain characteristics which seem to separate them from any known β. The calceoloid flattening of one ϵ individual (text-fig. 3*e'*) extends from the apex almost the full length of the corallite. This condition is compensated on the opposite side of the corallite but would necessitate derivation from a β with a compressed calyx rim. This individual is extreme but all gradations to the cylindrical form are known. However, all individuals showing this tendency are distinct ϵ's and no β's with the proper form are known. For this reason the ϵ individuals are not considered gerontic β individuals.

Form γ is rare, only 4 specimens being known, 2 each from New York and the Indiana-Kentucky localities. These form a link between form β, considered typical of the species, and form δ described by Davis as a variety of the species. *A. exiguum* var. *elongatum* Davis is more robust than form γ and is more rounded. The early calceoloid flattening is less pronounced and the change from pyramidal to cylindrical growth is gradual. It is apparently fairly common at the Indiana-Kentucky localities, 12 specimens being included in Davis' collection to 2 specimens of form γ. Form δ is sufficiently separable from form β to be considered a variety but its position in the α-β-γ-δ lineage is definite.

CAUSES OF INDIVIDUAL VARIATION

Individual variation in fossil and living corals has received some attention particularly as regards environmental control of growth form. Almost no studies have been made of variation within a given environment at a given time. Wells (1937) reviewed sparse earlier work and described 11 formae of *Heliophyllum halli*, Milne-Edwards and Haime, some of which had previously been described as species by Hall (1877). All of the formae were found at each of two localities and represent rather extreme variations in growth form within a single community. Wells listed the following factors as causing the variation in *H. halli* (1937, p. 18):

1. Reproductive precocity
2. Stability or instability
3. Gerontism
4. Irregular rejuvenescence
5. Differential growth rate

Of these factors only differential growth rate is certainly applicable to *A. exiguum* but it is possible that gerontism played some part.

Mayr, Linsley, and Usinger (1953, p. 81–99) provided a framework for study of variation within a living population. Wells (pers. comm.) has applied this scheme to *H. halli* in an informal talk and the writer found the scheme and its application to be very stimulating.

The following factors are of possible importance in *A. exiguum* (compare Mayr, et al., loc. cit.):

I. Extrinsic (noninherited) factors
  A. Progressive individual variation (only age variation is likely to be involved)
    1. Neanic forms (Possibly some α individuals)

2. Gerontic forms (Probably not a factor)

B. Ecological variation
   1. Micro-environmental (May be important in the development of continuous variation, see below, but can be only indirectly inferred in fossil populations)
   2. Density dependent (Different forms might result from food shortage produced by crowding)

II. Intrinsic (inherited) factors. (In corals must be non-sex associated)

A. Continuous variation (Due to slight genetic differences between individuals)
   1. Differential growth rates ($\alpha_1-\alpha_2$; $\beta-\zeta_1-\zeta_2$)
   2. Differential stage development ($\alpha-\beta-\gamma$; $\alpha-\beta-\epsilon$)

The wide variation in apical angles in *A. exigum*; is due to differing growth rates. As stated previously rapid polyp growth is related to a large apical angle and relatively slow polyp growth to a small one. More rapidly growing individuals would presumably mature earlier, and later activity would serve to lengthen the corallum with little diameter increase (e.g. form β). Form γ is an extreme example of the same tendency, and might be considered gerontic were it not for the existence of form δ (*A. exiguum* var. *elongatum*).

More slowly growing individuals would more slowly approach the mature size, and the conical form ζ would result. Form ζ_2 represents an extreme case where growth expansion was so slow that the mature size was not attained.

Stage acceleration is represented by form ϵ. This form proceeds from an α stage to a cylindrical stages as does form γ, but cylindrical growth begins at a smaller diameter perhaps indicating early maturation of the polyp.

Wide variation in form α is certainly due to differential growth rate. Some α individuals, however, seem identical to the α stage of β or ζ individuals and may represent a neanic stage of growth.

Form δ (*A. exiguum* var. *elongatum*) is not easily explained by any of the above factors. Changes here seem more fundamental, involving all ontogenetic stages, and the form is perhaps indicative of a genetic trend.

Most of the variation in *A. exiguum* seems to be due to slight genetic difference between individuals (II A above), but this is incapable of proof in fossil populations. Continuous variation could also be caused by extrinsic factors (I B 1 and 2 above). Such obvious things as food and oxygen supply, depth of water, and water movements would be generally uniform over the small area of a given locality, but small variations are inevitable and large variations between some micro-environments are possible.

For example, micro-environmental differences might be due to the position of individuals with respect to larger rugose and tabulate corals. Assumig a random distribution of *A. exiguum* and larger corals some of the former would inevitably be shaded by, or on the lee side of some of the latter. This would cause variations in amount of light, food, oxygen, etc. received by different individuals, but whether significant differerences would exist is not known. Theoretically, however, individuals favorably placed might grow rapidly (α-β-γ-δ lineage), while less well placed forms might grow more slowly (α_2-ζ_1) and poorly situated individuals might be stunted (ζ_2).

Similar results might be due to varying distribution density. Crowding might decrease the food supply per individual and thus cause a decrease in the rate of polyp expansion. Assuming adequate supplies of calcium carbonate the rate of corallite length increase would not be affected and a small apical angle would result. A wide density range could be responsible for the principal type of variation involved.

ACKNOWLEDGMENTS

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SOME LOWER CARBONIFEROUS BRACHIOPODS FROM THE VOLCAN FORMATION, SAN JUAN, ARGENTINA

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ABSTRACT—Eight species of Lower Carboniferous brachiopods from the Volcán Formation are described. Of these, *Streptorhynchus inaequiornatus* Lea. and *Septosyringothyris keideli* (Harr.) are known. *Chonetes* sp. cf. *C. chesterensis* Weller, *Camarotoechia chavelensis*, n. sp., *Reticularia punillana*, n. sp., *Septosyringothyris* sp. and "*Spirifer*" sp. are new. The genus *Sanjuania* is proposed.

INTRODUCTION

A VARIETY of brachiopods are distributed in the Lower Carboniferous Volcán Formation along the Sierra de Volcán, in the north of the province of San Juan, to the west of Guandacol (see location map). The material was collected by Dr. G. Furque of the Argentinian Geological Survey (Dirección Nacional de Minería), who recently described the geology of this area (Furque, 1956a,b).

The Volcán formation is a 500 meter thick succession starting with continental deposits containing plant remains (Furque, 1956b), grading into an upper section of graywackes, limestones and mudstones containing a marine fauna from which the brachiopods were taken. These are associated with gastropods, pelecypods, cephalopods, conulariids and ostracods. The brachiopods are of particular interest from a stratigraphical point of view, as some of them are found in other exposures of Lower Carboniferous rocks in Argentina, especially in the range of the "Precordillera of San Juan y Mendoza," and recently in Patagonia.

The brachiopods are not abundant in species or in individuals. No orthoids or terebratuloids were identified, and only one strophomenoid has been recorded; productoids are present, but due to their very imperfect preservation it has been impossible to identify them.

Evidence afforded by the brachiopods suggests a Lower Carboniferous age for the Volcán formation, although the scarcity of the material does not permit an exact age determination.

This work was carried on during a British Council scholarship as Research Associate in the Department of Geology, University of Glasgow. I am greatly indebted to Prof. T. Neville George who kindly read and criticized the manuscript. Also I want to express my gratitude to Dr. Helen M. Muir-Wood (British Museum) and Dr. G. Arthur Cooper (U. S. National Museum) for their helpful advice and criticism. My thanks are also due to Mr. A. Ferguson (Glasgow), Mr. E. Owen (British Museum) and Mr. A. Romero (University of Buenois Aires).

SYSTEMATIC DESCRIPTIONS

Genus STREPTORHYNCHUS King, 1937

STREPTORHYNCHUS INAEQUIORNATUS Leanza

Pl. 107, figs. 14–17

S. inaequiornatus Leanza, 1945, p. 286–291, pl. III, figs. 1–7; pl. IV, figs. 1–9; pl. V, fig. 6.

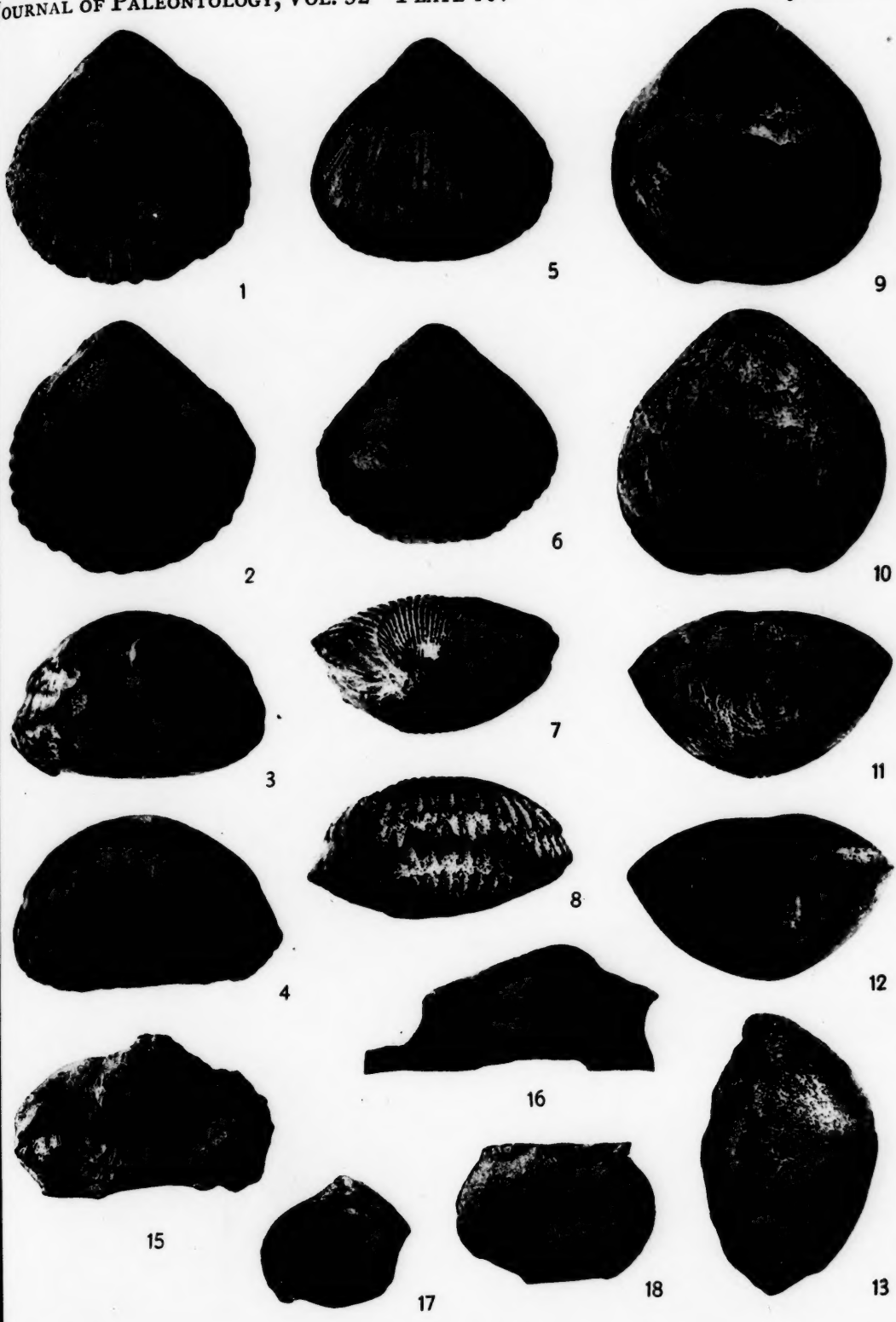
Observations.—The specimens from this

EXPLANATION OF PLATE 107

FIGS. *1–8—Camarotoechia chavelensis* Amos, n. sp. *1–4*, paratype No. DNM 494. *1*, ventral exterior; *2*, brachial exterior; *3*, posterior view; *4*, anterior view. *5–8*, holotype No. DNM 493, *5*, ventral exterior; *6*, brachial exterior; *7*, posterior view; *8*, anterior view, all ×2.

9–13—Sanjuania dorsisulcata Amos, n. gen. and n. sp., holotype No. DNM 487. *9*, dorsal exterior; *10*, ventral exterior; *11*, posterior view; *12*, anterior commissure; *13*, lateral view, all approx. ×2.

15–18—Streptorhynchus inaequiornatus Leanza. *15*, pedicle exterior ×1; *16*, interarea ×3; *17*, pedicle interarea and dorsal valve ×1; *18*, brachial exterior ×1.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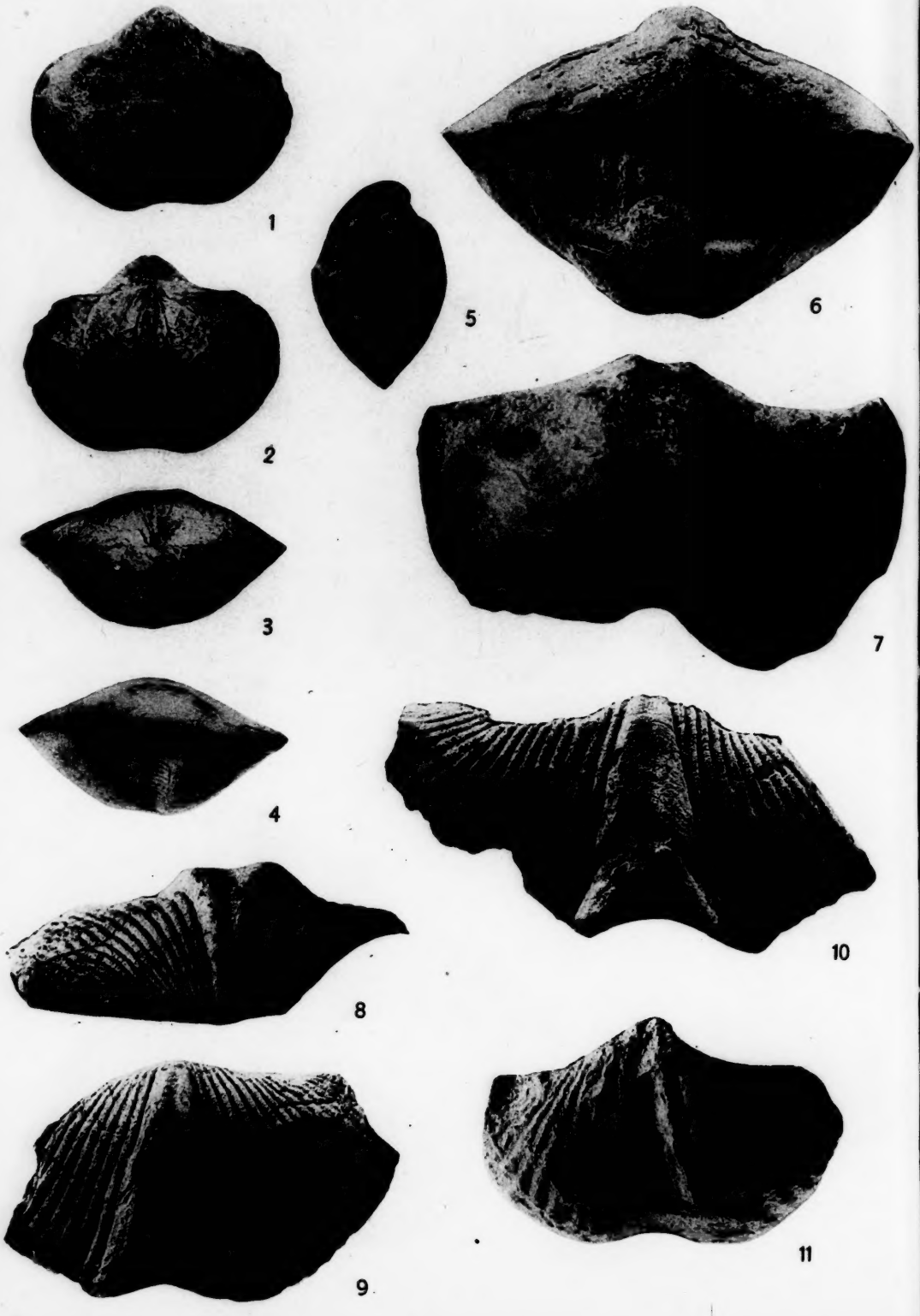
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locality are larger than the types from the Sierra de Pericó, San Juan (dimensions: width 34 mm., length 29 mm.). The area is small with rounded straight beak ridges; delthyrium closed by strong and convex pseudodeltidium. The difference in sculpture as shown in the types is rather subtle in our specimens, and the valves are usually not as deformed. The dorsal valve is convex, and interiorly the socket ridges extend one fourth the length of the shell.

Locality.—Portezuelo de Quebrada Las Playas, south of Puesto Chepical, 20 km. WSW of Guandacol.

Repository.—Dirección Nacional de Minería, Museo, No. 500.

Genus CHONETES F.v. Waldh., 1837, emend. Paeckelman, 1930

CHONETES sp. cf. C. CHESTERENSIS Weller

Description.—Pedicle valve small, semi-elliptical, slightly convex posteriorly; length two-thirds its width. Anterior margin rounded in outline. Hinge line less than maximum width, about the length of the valve. Cardinal extremities obtuse. Maximum width near the anterior third of the length. Umbo very small and slightly flattened. Area small and triangular with seven cardinal spines. Anterolateral margins rounded. Surface of valve covered with small angular costellae, separated by slightly wider intercostellae. Increase in costellae by bifurcation. 9–10 costellae in 1 mm. near the anterior margin. Internal characters unknown.

Dimensions.—Width 10 mm., length 7 mm., cardinal line 7 mm.

Observations.—Although the dorsal valve has not been found in our collections, the form described herein resembles *Chonetes chesterensis* Weller from the Chester group of Illinois (Weller, 1914, p. 83, pl. VIII, figs. 33–34), but differs in having a shorter hinge line.

Locality.—Quebrada Chavela, 25 km. to the north of Rodeo, San Juan.

Repository.—D.N.M. No. 497.

Genus CAMAROTOECHIA Hall & Clarke, 1893

CAMAROTOECHIA CHAVELENSIS Amos, n.sp.

Pl. 107, figs. 1–8; text-fig. 1

Diagnosis.—Medium sized, triangular to subpentagonal camarotoechids with uniplicate anterior margin. Sulcus and fold covered with 7–8 sub-angular costae, flanks with 8–12. Ventral interior with subparallel dental lamellae, strongly divergent anteriorly, extending one-sixth the length of the valve. Dorsal interior with divided hinge plate, extending around the length of dorsal valve.

Description.—External characters: Shell of medium size, rostrate, triangular to subpentagonal in outline. Umbonal angle 90° to 100°. Length equals width. Thickness around one half the width. Greatest width at midlength of shell. Maximum thickness near the posterior third of the shell. Anterior margin uniplicate and crenulated. Ventral valve with maximum convexity near the umbo, becoming flatter anteriorly. Median sized rounded umbo; shoulders slightly concave to flat. Foramen small. Posterolateral margins straight, lateral rounded at maximum width, anterior straight. Sulcus not well defined posteriorly from flanks, starting about midlength of valve, widening rapidly anteriorly to one half the width of the shell, depth one-fifth the thickness at the anterior margin. Flanks very convex along posterolateral margins, covered with subangular to rounded strong costae separated by subangular to angular intercostae. 12 costae on flanks, 8 in sulcus, all starting at the umbo, widening anteriorly, never bifurcating; those near the posterolateral margins obsolete and curving laterodorsally. Dorsal valve with an even convexity, but becoming slightly depressed or flattish near the umbo.

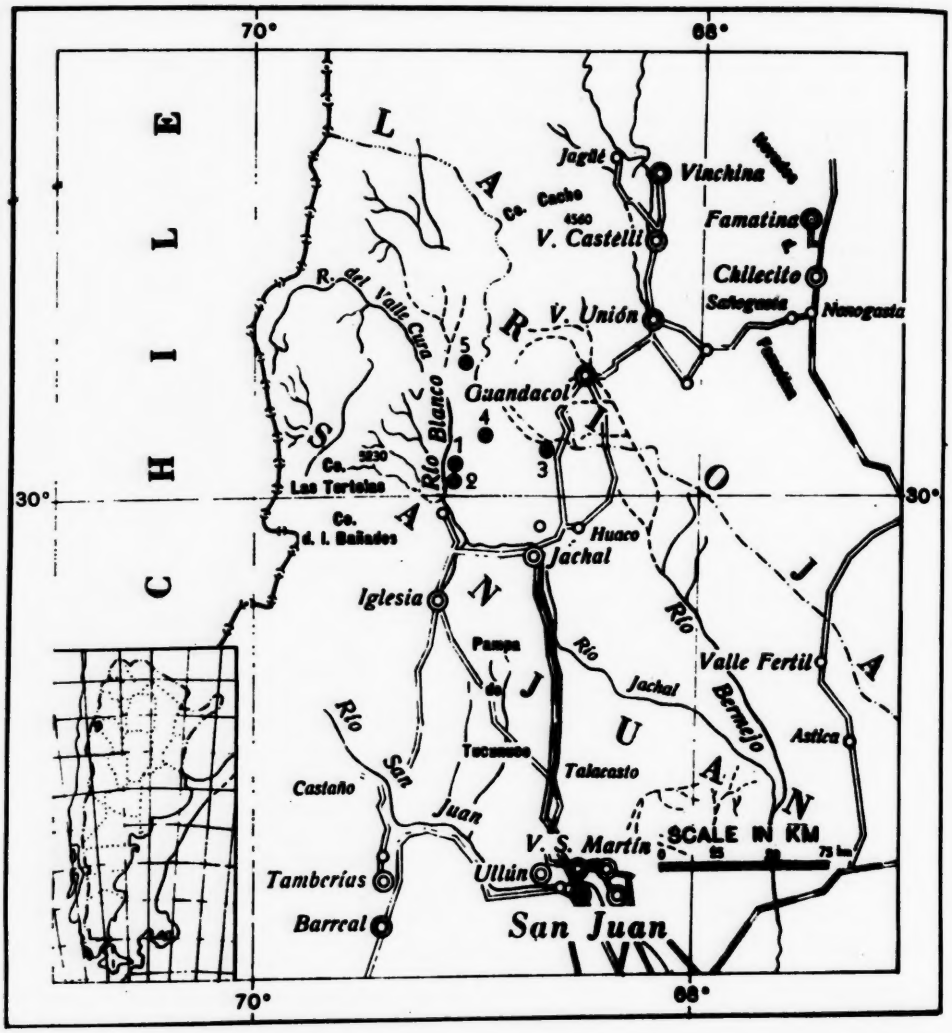
EXPLANATION OF PLATE 108

FIGS. *1–5—Reticularia punillana* Amos, n. sp., holotype No. DNM 491. *1*, pedicle exterior; *2*, brachial exterior; *3*, posterior view; *4*, anterior commissure; *5*, lateral view, all ×1.5.

6–7—Septosyringothyris keideli (Harr.) *6*, posterior view; *7*, pedicle valve, both ×1.5.

8–10—Septosyringothyris sp. *8*, posterior view of brachial valve; *9*, brachial exterior; *10*, brachial exterior of another specimen, all ×1.

11—"Spirifer" sp. Pedicle exterior ×1.5.



TEXT-FIG. *1*—Map showing fossil collecting localities in the Volcan Formation in northern San Juan. 1. Quebrada Cortadera; 2. Quebrada Chavela; 3. Quebrada Las Playas; 4. Vega El Volcán; 5. Quebrada El Salto.

Beak inconspicuous. Fold not defined, except at the anterior margin; with 8 costae. Flanks with 10–12 costae. Nature of costae as in ventral valve. Both valves bear well marked but few concentric growth lines.

Internal characters: Ventral valve with thin parallel dental lamellae, slightly, concave inwards posteriorly, strongly divergent anteriorly, extending one-sixth the length of the valve. Teeth strong and globular, situated on dorsal extremities of the dental lamellae. Dorsal valve with divided hinge plate; with deep concave dental sockets, covered posteriorly by a lateral extension of the hinge plate. Cruralium extending $\frac{1}{5}$ the length of the dorsal valve. Thin median septum extending one-third the length of the valve. Crura extending from the inner margins of the divided hinge plate, extending anteriorly. Cardinal process unknown.

Dimensions.—(in mm.).

	Holotype No. 493	*Paratype* No. 494
Width	19.0	20.7
Length (pedicle)	17.0	20.0
Length (brachial)	16.0	19.0
Thickness	10.4	13.2
Width of sulcus	11.5	12.5
Depth of sulcus	2.0	4.5

Remarks.—The specimens within this collection display variations in their relative proportions. There are globose to rather flattish forms; from the latter we have chosen the holotype. The thickness-width relation in the globose forms is about two-thirds, in the other forms it is about one-half. The depth of sulcus to width is one-fourth in the globose to one-ninth on the remainder. In smaller specimens the sulcus is not well defined, showing only a gentle plication at the anterior margin.

Our form resembles very closely *C. nitidula* Stainbrook from the Aplington Dolomite, Iowa (Stainbrook, 1950, pl. 54, figs. 30–34), but it differs in shape and dimensions. *C. sobrina* Stainbrook from the Percha shale (Stainbrook, 1947, pl. 47, figs. 19–22) is also similar in shape but the number of costae on fold and sulcus is larger in our species. *C. griasica* Naliv. from the Moscow Basin (Sarytcheva & Sokolskaya, 1952) has a more globose form and smaller number of costae in the fold and sulcus.

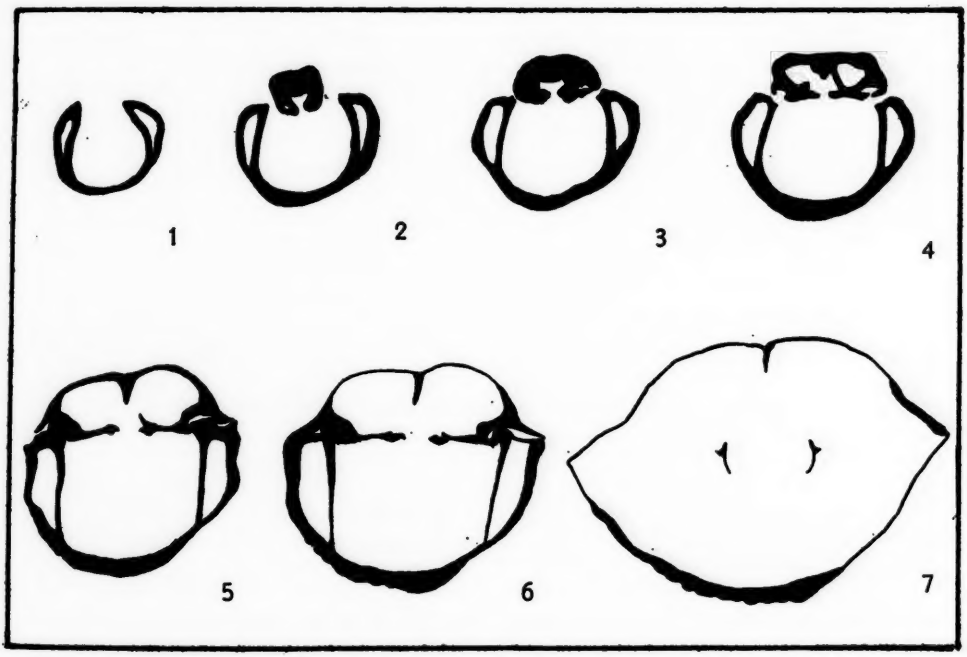
Locality.—Quebrada Chavela and Quebrada Cortadera, San Juan.

Repository.—D.N.M., Holotype No. 493 (pl. 2, figs. 5–8); figured paratype No. 494 (pl. 2, figs. 1–4); unfigured paratype No. 495.

Genus SANJUANIA Amos, n.gen.

Diagnosis.—Median sized to small, smooth leiorhynchids, with rectangular fold on ventral valve and sulcus on dorsal. Ventral interior with short parallel dental lamellae. Dorsal interior with small divided hinge plate, almost sessile septalium. Shell structure impunctate.

Type species.—*Sanjuania dorsisulcata* Amos, n.sp.



TEXT-FIG. *2*—Sections across the ventral valve of *Camarotoechia chavelensis* Amos, n. sp., about ×4; Distance of sections from apex: *1*, 1 mm.; *2*, 1.58 mm.; *3*, 1.76 mm.; *4*, 1.87 mm.; *5*, 2.4 mm.; *6*, 2.6 mm.; *7*, 3.63 mm.

SANJUANIA DORSISULCATA Amos, n.sp.
Pl. 107, figs. 9–13; text-fig. 3—8,9,13

Description.—External characters: Shell biconvex, globose and subcircular in outline. Length equals width. Posterolateral margins rounded. Maximum width and thickness at two-thirds and one-half the length of the shell respectively. Anterior margin sulcate. Fold, sulcus and flanks with fine concentric growth lines. Pedicle valve evenly convex with medium sized beak, slightly incurved over area, and close to beak of brachial valve. Area very small and anacline. Foramen large and circular, submesothyrid. Fold inconspicuous near the umbo, distinct near the anterior margin, merging into the flanks and not abruptly limited; height one third its width at the anterior margin. Flanks evenly convex. Brachial valve flatter than ventral. Beak very small and pointed. Sulcus broad anteriorly, with rounded margins, starting at the posterior third of valve and increasing rapidly towards the anterior margin. *Internal characters:* Pedicle valve with short parallel dental lamellae, extending 1 mm. (one-twentieth of the length of the valve). Brachial valve with small concave divided hinge plate. Socket plates divergent. Median ridge small, starting 1 mm. from the beak and extending about one-seventh the distance towards the anterior margin.

Dimensions.—(in mm.).

Width	20.8
Length	20.4
Thickness	13.0
Width of sulcus	10.2
Depth	3.7

Remarks.—The anterior margin is distinctly sulcate. In smaller specimens it is only a gentle warp, and sometimes inconspicuous, although the fold is nearly always better observed than the sulcus. Unfortunately the ornamentation cannot be seen clearly in the specimens at hand, as all of them are partly exfoliated.

Sanjuania n.gen. is related to *Paranorella* Cloud (1944), but the latter has a longer median septum and a troughed cardinal plate. Dr. G. A. Cooper (personal communication) states that the internal structure is identical with that of *Nudirostra*, and that species of the genus *Neorhynchus* and *Abysothyris* are indistinguishable on exterior characters with the species here described.

Locality.—Vega de las Cuevas, 46 km. to the W. of Guandacol, and Vega El Volcán, Prov. of San Juan.

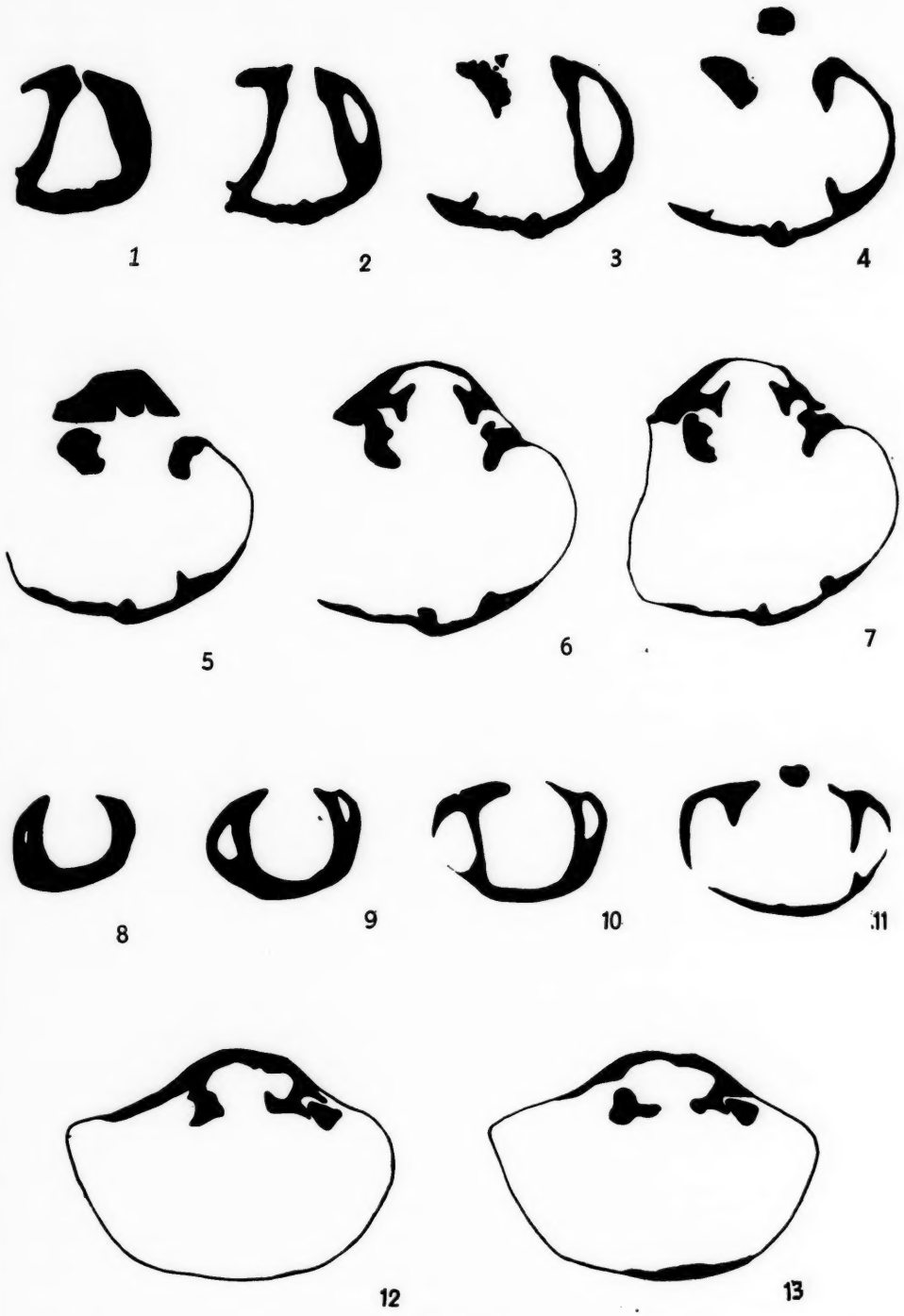
Repository.—D.N.M. Holotype No. 487 (pl. 1, figs. 9–13). Unfigured paratype No. 489.

Genus RETICULARIA M'Coy, 1844
RETICULARIA PUNILLANA Amos, n. sp.
Pl. 108, figs. 1–5; text-fig. 3—1–7

Diagnosis.—Shell transversely elliptical with uniplicate anterior margin, short divergent dental lamellae and low median ridge in the ventral valve.

Description.—External characters: Shell biconvex, dorsal valve flatter than ventral. Length four-fifths of the width. Cardinal extremities rounded. Hinge line straight about two thirds the maximum width. Anterior commissure uniplicate. Pedicle valve with prominent beak, pointed and incurved. Area narrow, curved and apsacline, height about one-sixth its width. Sulcus shallow, smooth, with gentle and rounded margins, prominent near the anterior margin, where it is one-third the maximum width; depth of sulcus at anterior margin about one-ninth the width. Lateral flanks convex near the cardinal line, but flat along the anterolateral margins; marked with fine concentric growth lines set at intervals of about 0.3 mm. apart and holding the so called uniramous spine bases, not as well preserved, about 9–10 in 1 mm. Spine bases not continuous on succeeding growth lamellae. Brachial valve subrectangular. Beak and area inconspicuous. Fold (mesial swelling) flat and starting at midlength of valve, broadening rapidly to about 60°.

Internal characters: Pedicle valve with slightly convex inwards dental lamellae diverging at an angle of 35°, extending 3 mm. from the umbo, not beyond hinge line, with concave anterior edges. Very fine median ridge (non euseptoid) extending to one-third the length of the valve. Teeth strong. Brachial valve with divided small hinge plate. Cardinal process with longitudinal striae. Dental sockets deep. Muscular impresions on posterior one-fourth of the valve, elongate and divided by a faint



TEXT-FIG. *3*

1–7—Reticularia punillana Amos, n. sp. Sections across the valves. Distance of sections from apex: *1*, 2 mm.; *2*, 2.48 mm.; *3*, 3.4 mm.; *4*, 4 mm.; *5*, 4.4 mm.; *6*, 4.8 mm.; *7*, 5 mm. All figures ×3.6.
8–13—Sanjuania dorsisulcata Amos, n. gen. and n. sp. Distance of sections from apex: *8*, 0.35 mm.; *9*, 0.84 mm.; *10*, 1 mm.; *11*, 1.15 mm.; *12*, 2 mm.; *13*, 2.2 mm. All figures 3.6.

ridge, extending one-third the length of the dorsal valve. Crura attached to bases of socket supports. Spiralia directed posterolaterally with four to five coils.

Dimensions.—(in mm.)

	Holotype	Paratype
Width	27.3	12.2
Length (ventral)	22.0	10.0
Length (dorsal)	18.0	9.0
Thickness	13.8	5.9
Cardinal line	18.0	6.0
Height of area	2.7	—
Width of sulcus	9.0	—
Depth of sulcus	1.2	—

Remarks.—The present species is comparable with the lectotype of *Reticularia imbricata* Sow. (British Museum, Sowerby collections No. 62173) from the Upper Avonian (D_2) of Yorkshire, but it differs from this species in its transversely elongated shape, shorter spacing of the growth lamellae and internally in the absence of a median septum. Only a small ridge dividing the muscle impressions has been observed (text-fig. 3). It differs from *R. notica* C. Reed (1927) from the Quebrada del Salto, Barreal, San Juan, Argentina, externally by the subrectangular shape of the valve. *R. punillana*, n. sp., is also comparable to *R. sinuata* Tolmatchoff (1931) from the Kouznetsk basin, Altai, Siberia but the area is higher, nearly equilateral, and the outline is more like *R. imbricata* Sow.

Locality.—Vega de las Cuevas, near Vega El Volcán.

Repository.—Holotype D.N.M. No. 491; unfigured paratype No. 491a.

Genus SEPTOSYRINGOTHYRIS Vandercammen, 1955

SEPTOSYRINGOTHYRIS KEIDELI (Harrington)
Pl. 108, figs. 6–7

Syringothyris keideli (Harr.) Keidel & Harrington, 1938, p. 114, pl. 5, figs. 1a–d, text-fig. 2.
Syringothyris keideli (Harr.) in Dessanti, 1945, p. 214.
Syringothyris keideli (Harr.), in Zöllner, 1950, p. 112.
Septosyringothyris keideli (Harr.) Amos, 1957, p. 000.

Description.—Complete specimens, some of them deformed, were found to agree with the type from Leoncito Encima (Keidel & Harrington, 1938) but the cardinal area is slightly higher, about one-third the hinge line, and the valves are thicker. Comparisons have also been made with the specimens found by Zöllner (1950) in the Cordón del Naranjo a few kilometers south of the type locality, showing external differences in shape, although internally the divergence and extension of the dental lamellae and median septum do not show any remarkable difference.

Dimensions.—(in mm.)

	No. D.N.M. 496	No. D.N.M. 496a
Width	30	52
Length of ventral	22.0	40.3
Length of dorsal	19.5	35.5
Thickness	16.0	34.3
Height of area	8.0	11.5
Hinge line	26.0	45.0
Width of delthyrium	8.5	—
Width of sulcus	10.5	11.5
Depth of sulcus	4.0	

Locality.—Quebrada del Salto, E of Río Blanco, San Juan.

Repository.—D.N.M., Museo. No. 496.

SEPTOSYRINGOTHYRIS sp.
Pl. 108, figs. 8–10

Description.—Shell transversely elongate, slightly alate; length four-fifths its width. Pedicle valve subconical. Area apsacline, triangular, slightly curved near the apex. Apical angle 130°. Umbo pointed. Delthyrium triangular, delthyrial angle 45°. Sulcus U-shaped, smooth, sharply defined from the flanks, widening anteriorly, one-third the width at the anterior margin; median line along its floor convex. Flat lateral flanks with 15–16 subangular costae, diminishing in width towards the cardinal extremities. Brachial valve evenly convex, umbo inconspicuous. Area small and linear. Fold smooth, subquadrate in cross section, depressed along its median line and slightly concave. Flanks rather flat, with 17 well marked subangular costae. Growth lines well marked at long intervals.

Remarks.—This form is distinguished from other known species by the transversely elongated shape, and the subquadrate, slightly concave fold. Unfortunately the material at hand is not sufficiently diagnostic to create a new species. On the other hand, examination of specimens of *S. keideli* (Harr.) from other localities show a strong variation within the same horizon, therefore

future and more abundant collections will help to decide the possibility of its inclusion as a new species.

Dimensions.—(in mm.)

Length of ventral valve	30
Hinge line	70
Height of area	24
Apical angle	180°
Delthyrial angle	45°

Locality.—Portezuelo de Quebrada Las Playas.

Repository.—D.N.M., No. 499.

"SPIRIFER" sp.
Pl. 108, fig. 11

Description.—Pedicle valve spiriferoid, transversely elongated, length one-half its width, cardinal extremities probably rounded; hinge line less than maximum width. Beak medium sized, slightly incurved over area; beak ridges slightly concave. Anterior commissure uniplicate. Sulcus not very deep, U-shaped, starting at the beak about one-fourth the width of the shell at the anterior margin, showing no traces of costulation. Flanks evenly convex, rather flattish near the anterolateral margins, with 8 well marked subangular costae, separated by smaller intercostae.

Remarks.—There is only a pedicle valve, that interiorly shows faint indications of possessing dental lamellae very close together forming the so called sessile spondylium, or a high and thick median septum. Unfortunately imperfect preservation does not permit an exact identification.

Dimensions.—Width, 41 mm.; length, 25 mm.; and width of sulcus, 12 mm.

Locality.—Portezuelo Quebrada Las Playas, south of Puesto Chepical.

Repository.—D.N.M., No. 408.

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INVERTEBRATE FOSSILS FROM THE LOWER CARBONIFEROUS OF NEW SOUTH WALES

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ABSTRACT—Fourteen species of Lower Carboniferous fossils are described from a dark calcareous mudstone in the upper part of the Lower Burindi group of northeastern New South Wales. Eleven species and one subspecies are new. There are species of tetracoral, *Cyalthoclisia lexicolumnaris*, n. sp., 11 species of brachiopods, *Rhipidomella fortimuscula*, n. sp., *Schizophoria verulamensis*, n. sp., *Leptagonia*, sp. cf. *L. analoga* (Phillips), *Pustula abbotti larga*, n. subsp., *Chonetes gloucesterensis*, n. sp., *Pliocochonetes sexifidus*, n. sp., *Phricodothyris campbelli*, n. sp., *Phricodothyris* sp., *Spirifer lirellus*, n. sp., *Tylothyris planimedia*, n. sp., *Punctospirifer amblys*, n. sp., one species of goniatite, *Beyrichoceras* sp., and a trilobite species, *Linguaphillipsia divergens*, n. sp. Paleoecology of the fauna is briefly discussed. The above species suggest an upper Tournaisian age.

INTRODUCTION

MOST of the forms of this study are brachiopods, but also included are a tetracoral, a trilobite, and a goniatite. Because of time restrictions, only those brachiopods were studied which seemed more conspicuous, more nearly completely preserved, and thereby more readily usable for future stratigraphical mapping. The other forms described were included as further substantiating evidence for age determination. The fossils described represent but a small fraction of the total fauna. There remain yet to be studied additional species of brachiopods and corals. Numerous species of pelecypods, gastropods, bryozoans, and a few representatives of other groups, have as yet been untouched.

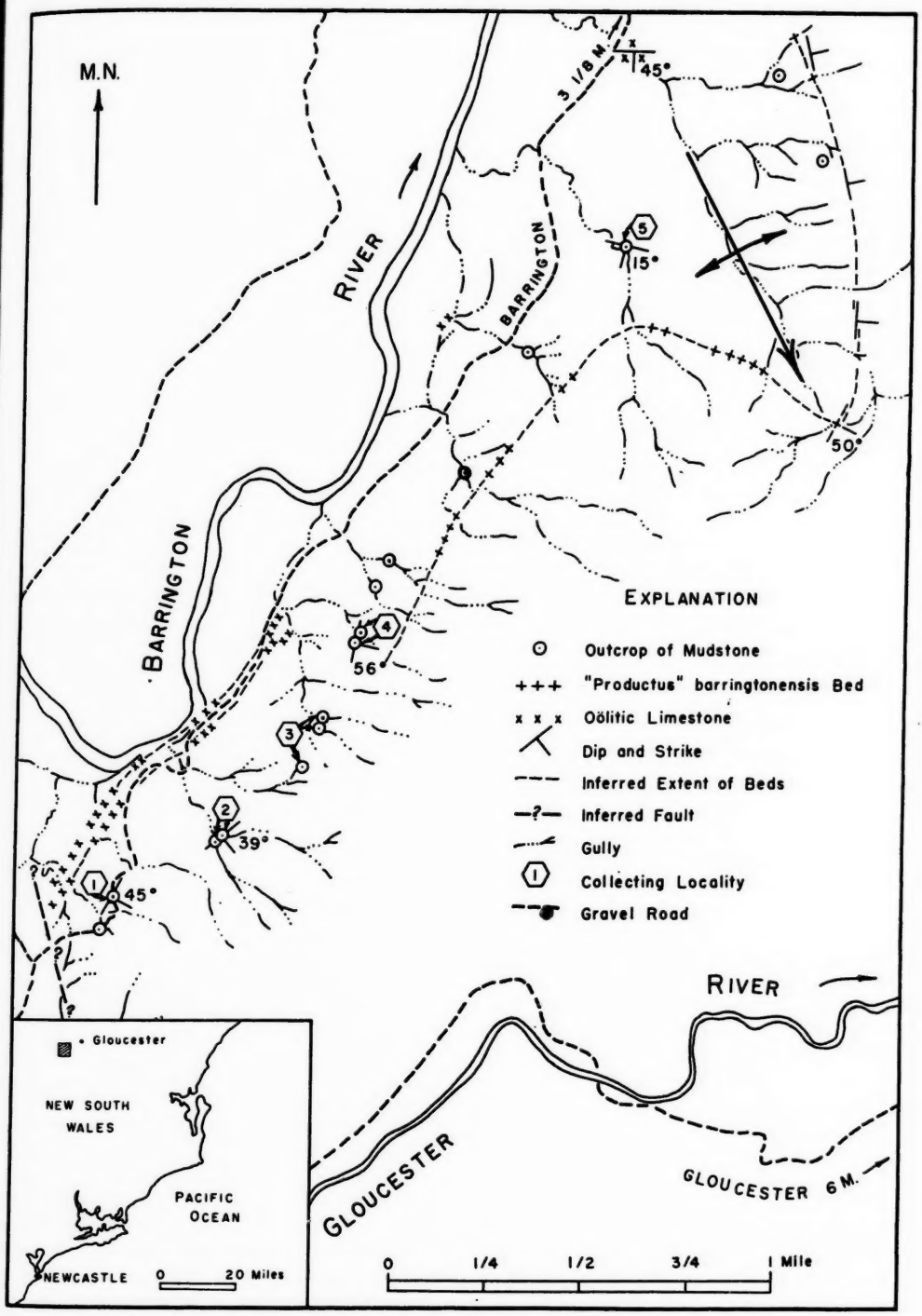
The fossils were collected in the Barrington-Gloucester area, approximately 75 miles north of Newcastle, in northeastern New South Wales (see text-fig. 1).

The area of the present study is on the west flank of an approximately north-south trending syncline, the Gloucester Trough, which plunges to the south. Fossils were obtained from the collecting localities listed below. The initial numeral refers to text-fig. 1; the L. number following each locality description is the accession number of the University of New England.

1. Exposure on east side of Harrington-Rawdon Vale road; grid reference 905362, Gloucester One Mile Sheet, 6¼ miles south of Barrington, N. S. Wales (L. 145).
2. Two small exposures in separate gullies, near junction of them; grid reference 911364, Gloucester One Mile Sheet, 6 miles south of Barrington, N. S. Wales (L. 146).
3. Exposure in two small gullies and on slope between gullies; grid reference 915367, Gloucester One Mile Sheet, 5⅞ miles south of Barrington, N. S. Wales (L. 147).
4. Small dam excavation and small gully; grid reference 916372, Gloucester One Mile Sheet, 5 miles south of Barrington, N. S. Wales (L. 66).
5. Small gully exposure where fossiliferous mudstone overlies a thin pitchstone; grid reference 931387, Gloucester One Mile Sheet, 3¾ miles south of Barrington, N. S. Wales (L. 148).

Little detailed paleontology has been done on marine Burindi fossils in the immediate Barrington-Gloucester area. The first marine fossil described was *Productus barringtonensis* by Dun in 1902b; this species was collected "at the 'Washtubs,' near Barrington. . . ." Campbell (1956) revised this species and assigned it to the genus *Marginirugus;* he also erected a subspecies, *M. barringtonensis alatus*. Other marine paleontology in this area consists only of faunal lists (Sussmilch, 1921; Voisey, 1940). Sussmilch (p. 245–246) listed 10 species of brachiopods, a trilobite, a *Zaphrentis*, and crinoid stems. Voisey divided the Burindi rocks into four zones based on fossil assemblages. The fauna of the present paper was included in the "V" zone, from which Voisey listed the following brachiopods: "*Leptaena analoga*," *Productus* sp., *Spirifer pinguis*, and *Spirifer striata*.

Fossils were collected from a dark cal-



TEXT-FIG. *1*—Location map of studied area near Gloucester, New South Wales, showing collecting localities and marker beds. Small ruled area in inset shows position of location map.

careous fairly homogeneous mudstone in the upper part of the Lower Burindi group. Relationship of the Lower Burindi with other Carboniferous rocks can be obtained from Campbell (1956, p. 463) or from Carey and Browne (1938). This mudstone has been measured approximately at collecting localities shown as 1 and 2 in text-fig. 1. Averaging the measurements from the two localities reveals an approximate thickness of 107 feet. Outcrops are small and restricted, being incompletely exposed and found mostly in the deeper gullies. Occasionally, fragments of this rock were found in isolated areas on the slopes between gullies. It is so extremely fossiliferous that on no occasion was a fragment of this rock noted which did not contain some fossils.

The stratigraphical position of the mudstone can be rather easily determined in the field (see text-fig. 1). Approximately 150 feet stratigraphically above, is the "*Productus*" *barringtonensis* bed, a "coarse feldspathic tuff" with numerous molds of the characteristic productid. Approximately 150 feet stratigraphically below the mudstone are two thin, oölitic limestones separated by a very thin mudstone with a characteristic fauna, which includes a large chonetid, *Daviesiella aspinosa* (Dun). Campbell (personal communication, April 30, 1957) considers this species a primitive representative of the genus, and the species is thought to indicate an upper Tournaisian age for the bed. The fossiliferous mudstone currently studied can then be picked as the only mudstone between the "*Productus*" *barringtonensis* bed and the two thin, oölitic limestones.

No attempt was made to measure a complete stratigraphic section of the area for several reasons. First of all, the rocks in the studied area have, as yet, not been separated into formations. It is the author's opinion that with this study, and with other faunal studies to follow, stratigraphers will be in a better position to draw formational boundaries. Until the time comes for formational designation, it does not seem necessary to measure a complete, accurate section. Also, sections with approximate thicknesses have been measured and described in this area by Voisey (1940), subsequent to the original sequence of rocks given by Sussmilch in 1921. The mudstone of this study is "horizon VI" in the Cut Hill Section of Voisey (1940, p. 199).

PALEOECOLOGY

As mentioned previously, outcrops of the fossiliferous mudstone are limited largely to small restricted exposures in gullies. Therefore, the writer was not able to determine with certainty the distribution of fossils throughout the thickness of the bed. A cursory examination, however, revealed no apparent zonation of species throughout the thickness of the mudstone.

Little of the paleoecological data obtained was treated quantitatively. Associations of fossil forms, their positions of preservation, and other characteristics were noted when the fossils were freed from the mudstone for study. Also, considerable data was gathered from a mudstone slab, about 2 feet by $1\frac{1}{3}$ feet, that was collected from near the base of the mudstone bed. That which follows applies to brachiopods unless otherwise stated.

The larger proportion of fossils collected from the various localities and as shown on the mudstone slab is represented by dissociated valves. On the slab were noted 189 brachiopod valves (exclusive of the brachial valves of *Leptagonia*), which were, or were presumed to be, dissociated. Sixty-two per cent of these valves had the convex surface up and thirty-eight per cent had the convex surface down. Brachial valves of *Leptagonia* were not included in this census, for it is believed these valves may be equally stable in either position because of the low general convexity, and the pronounced marginal flange. Brachiopods with biconvex connected valves were also present, but were excluded from the count for obvious reasons.

There was no evidence of current sorting of species. Species were thoroughly mixed; occasionally, some species were more common in some small restricted areas, but there was no apparent predominance of any one species over another. Specimens also did not have any preferred anterior-posterior alignment, but were randomly oriented. There was no evidence of strong or frequent

overlapping of specimens, *i.e.*, no evidence of strong "piling" action.

Most specimens showed in detail those structures necessary for complete description. Distortion was common, very likely due to compaction of the sediment during lithification. Fragmented valves were not common and worn shells were rarely encountered. However, long fragile structures such as spines were usually broken from their points of attachment. Long, rather coarse spines of *Dictyoclostus* sp. were usually absent from the valves, but were frequently seen isolated in the containing rock. Also, no chonetids were discovered with all their cardinal spines intact. Only partial spines were noted, and these were more nearly complete near the beak, possibly because of the protection afforded by this portion of the shell.

Fenestrate bryozoans were rarely complete, occurring commonly as fragments with broken irregular edges. Solitary corals were usually found with the axis lying parallel, or nearly so, to the bedding. No specimens noted could be said to be in a living position.

Effects of transportation of the fauna are indicated by several factors. Among them are the large proportion of dissociated valves, the greater proportion of those valves with their convex surfaces uppermost, and the separation of spines from those forms having long, fragile structures of this kind. In brief, the general appearance of the fossils suggests movement. Specimens were usually very abundant, giving the impression of overcrowding.

Although transportation of shells is quite evident, it is suggested that they were not moved far from their position of growth. Evidence for this is the common occurrence of young individuals and the common preservation of rather delicate structures, such as the teeth on isolated valves. Also, valves seldom show effects of wear, except for the breakage of spines. Solitary corals, however, occasionally show abrasive wear of the corallite, especially in *Cyathoclisia laxicolumnaris*, n. sp., the largest species. Possibly larger forms are more readily susceptible to wear than the generally smaller and differently shaped species of brachiopods.

From the data presented, the writer suggests the following interpretations. This fossiliferous mudstone was deposited in a shallow protected portion of the sea, free from strong current action, and from the sandy sediment which is common in the littoral zone of a coastal margin. The faunal association seems quite reasonable for an environment that was relatively constant and where life was flourishing. It seems likely that after death the animals were locally concentrated. The rather great thickness of the mudstone also appears to support the idea that the fossils are contained in what represents a living environment for them.

AGE OF THE FAUNA

Where rather close comparisons with faunas overseas have been made, on upper Tournaisian age for the present fauna is indicated. Those forms with which comparisons have been made are as follows: *Spirifer lirellus*, n. sp., is closely comparable with *S. logani* Hall from the Keokuk limestone (Osagean) of the United States. *Chonetes gloucesterensis*, n. sp., resembles *C. illinoisensis* Worthen from the Burlington and Keokuk limestones (both Osagean). *Schizophoria verulamensis*, n. sp., appears related to *S. swallovi* (Hall) from the Burlington limestone. Of Belgian species, *S. verulamensis*, n. sp., resembles most closely that variety of *S. resupinata* (Martin) called *rotundata*, which occurs in the upper Tournaisian or in the lowermost Viséan. *Rhipidomella fortimuscula*, n. sp., is similar to *R. burlingtonensis* (Hall) from the United States Osagean. *Beyrichoceras* sp., as studied, suggests an upper Tournaisian age at present, if comparisons are made with the United States. However, the upper boundary of the range of this genus has as yet not been determined, and generic comparisons are possibly of little value. Correlation with Europe, using *Beyrichoceras*, would be in conflict with the previous correlation, for this genus does not occur below the Viséan in Europe.

Further indications of an upper Tournaisian age is shown by comparisons with certain species in Australia. *Phricodothyris campbelli*, n. sp., and *Phricodothyris* sp. are closely comparable with *P. triseptata* Campbell and *P. uniplicata* Campbell, respec-

tively, from the upper Tournaisian at Babbinboon, N. S. Wales. *Schizophoria* sp. cf. *S. resupinata*, *Leptagonia analoga* (Phillips) and *Chonetes careyi* Campbell from Babbinboon are also related forms.

ACKNOWLEDGMENTS

This study was carried out from August 1956 to August 1957 under a Fulbright Grant, which was received while the author was undergoing postgraduate work at the University of North Dakota.

The writer thanks the following persons for their assistance in the preparation of this paper. Mr. K. S. W. Campbell, University of New England, Armidale, N. S. Wales, suggested the problem, kindly read the manuscript, and gave invaluable aid both in the laboratory and in the field. Professor A. H. Voisey, University of New England, placed the facilities of the geology department entirely at the writer's disposal. Mr. F. D. Holland, Jr., University of North Dakota, kindly read the manuscript, and aided the writer in the final completion of the present work. Dr. Dorothy Hill, University of Queensland, aided in the determination of the coral. Dr. H. M. Muir-Wood, Deputy Keeper, British Museum, donated brachiopod specimens for sectioning. Mr. H. O. Fletcher, Deputy Director, Australian Museum, made and donated plaster and rubber casts of type specimens. Mr. W. J. E. Webster, Zoology Technician, University of New England, gave technical advice and aid in the photography. Miss Nympha Gonzalez typed the manuscript.

SYSTEMATIC DESCRIPTIONS

Phylum COELENTERATA Frey & Leuckart, 1847

Subphylum CNIDARIA Hatschek, 1888

Class ANTHOZOA Ehrenberg, 1834

Order RUGOSA Milne-Edwards & Haime, 1850

Suborder STREPTELASMATINA Wedekind, 1927

Superfamily ZAPHRENTIDAE Milne-Edwards & Haime, 1850

Family AULOPHYLLIDAE Dybowski, 1873

Subfamily AMYGDALOPHYLLINAE Grabau *in* Chi, 1935

Aulophyllidae with a deepened fossula that is lengthened or expanded axially in the tabularium; septa are very numerous (after Hill, 1956, p. 290).

Genus CYATHOCLISIA Dingwall, 1926

Type species.—*Cyathoclisia tabernaculum* Dingwall, 1926, p. 12–21, pls. 1–3.

Diagnosis.—"Simple, Rugose [*sic*] corals, with a central column which is not defined by a bounding wall, but projects from the calyx as a highly-pitched, tent-shaped structure formed of a median plate, of very crowded, flattened, steeply-inclined tabellae, and of septal lamellae which are continuous with the major septa. The major septa are more or less twisted distally. There

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EXPLANATION OF PLATE 109

All figures are ×1 unless otherwise stated. Specimen F. numbers are those of the University of New England Collections. All specimens figured are from collecting locality L. 66.

FIGS. *1–6*—*Cyathoclisia laxicolumnaris*, n. sp. *1,2*, holotype, negative and positive prints, respectively, of a transverse section cut near the base of the calyx; note the loose axial structure, ×2, F. 3422A; *3*, paratype, rubber cast of the calyx showing the axial boss bisected by a median plate, F. 3427; *4*, vertical section through the upper portion of the corallite showing the axial boss (negative print), ×2, F. 3430; *5*, vertical section showing steeply inclined dissepiments and broadly arched outer tabulae; inner series of tabellae are not preserved, ×2, F. 3429A; *6*, paratype, vertical section cut normal to the median plate showing inner and outer series of the tabularium, ×2, F. 3423A.

7–13—*Rhipidomella fortimuscula*, n. sp. *7,8*, holotype, pedicle mold of the interior, and rubber cast of the same, F. 3442; *9*, paratype, brachial mold of the interior, F. 3445A; *10*, paratype, rubber cast of the brachial interior showing the cardinalia and adductor muscle imprints, F. 3444; *11*, paratype, brachial exterior, F. 3447; *12–13*, paratype, pedicle mold of the interior, and cast of the same, F. 3443.

14–16—*Schizophoria verulamensis*, n. sp. *14,15*, holotype, rubber casts of the pedicle exterior and interior, respectively, F. 3677A, F. 3677B; *16*, paratype, mold of the brachial interior, F. 3680.

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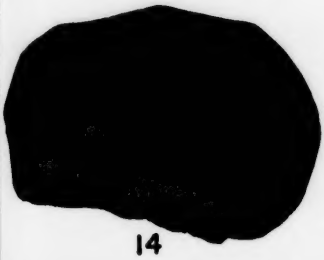
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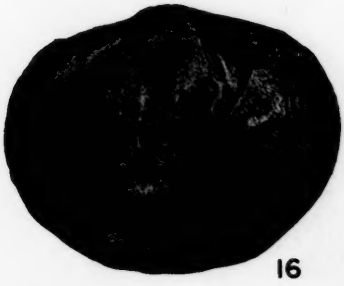
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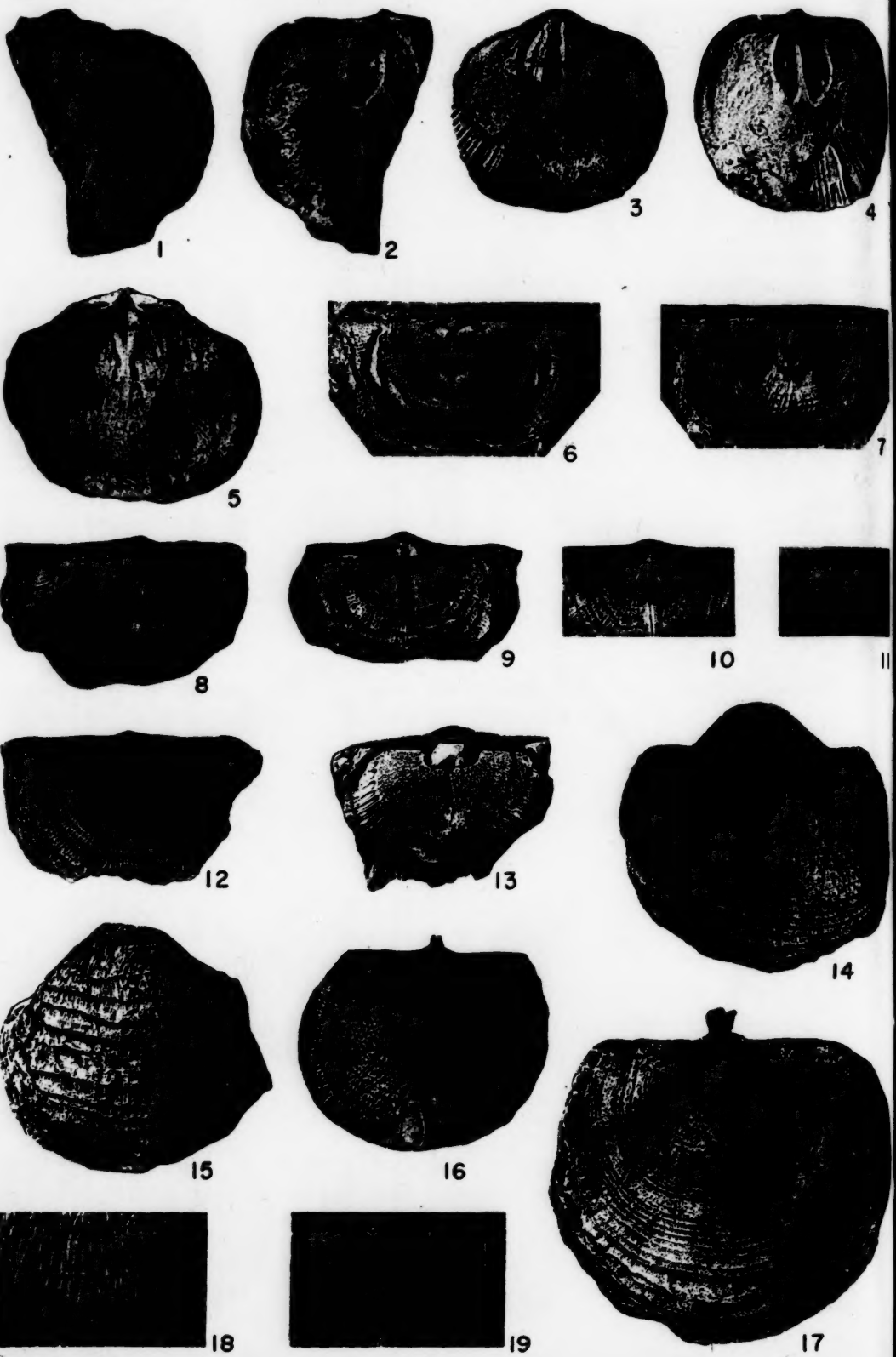
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is a well-marked and long cardinal fossula occupied by a long cardinal septum, the other fossulae being absent or inconspicuous. There is a wide dissepimental zone, and an intermediate tabellar zone." (Dingwall, 1926, p. 13).

Remarks.—Clisiophyllum Dana (1846) is similar, but has a short cardinal fossula, and a wall defining the axial column. *Turbophyllum* Parks (1951) differs in having a much weaker axial structure and pinately arranged septa near the cardinal fossula.

Cyathoclisia occurs in the Tournaisian of the South-West of England and South Wales, horizons γ and C of Vaughan (1905).

CYATHOCLISIA LAXICOLUMNARIS, n. sp.
Pl. 109, figs. 1–6

Diagnosis.—Corallum commonly curved trochoid; axial column loose, of relatively few curved septal lamellae, and tabellae; outer series of tabularium of broadly arched, incomplete tabulae; inner series of more numerous tabellae, broadly tent-shaped to rather highly arched.

Types.—Holotype, F. 3422A–F, L. 66; paratypes, F. 3423A–C, and F. 3424-F. 3427, L. 66; University of New England Collections.

Material.—F. 3422-F. 3441,. L. 66, includes two specimens cut transversely into serial sections, three vertical sections, few incomplete specimens of the corallite, and fragments of polished sections; University of New England Collections.

Description.—Exterior: The simple corallum is commonly curved trochoid, although some specimens approach a curved ceratoid shape. The largest specimen noted had a length of about 110 millimeters and a diameter of about 38 millimeters; the diameters of the holotype, near the base of the calyx, are about 24 by 27 millimeters. Fine transverse growth striations cover the surface of the epitheca, frequently crowding together to form coarser, irregularly spaced wrinkles. Shallow, rounded septal furrows, separated by broader interseptal ridges, are present on the apical portion of the corallum but fade out distally. A low rounded ridge on the convex side of the corallum marks the position of the long, deep cardinal fossula. Enclosed within an axial pit in the deep calyx is a prominent broadly arched to bluntly pointed calcicular boss, which is bisected by a long median plate in the plane of symmetry. A calcicular platform slopes gradually upward from the axial pit to the periphery of the calyx.

Interior: Near the base of the calyx in the holotype (diameters ca. 24 by 27 millimeters there are 63 major septa and a similar num-

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EXPLANATION OF PLATE 110

All figures are ×1 unless otherwise stated. Specimen F. numbers and collecting locality L. numbers are those of the University of New England.

FIGS. *1–5—Schizophoria verulamensis*, n. sp. *1,2*, paratype, pedicle mold of the interior, and rubber cast of same, showing the diductor muscle field and pallial markings, F. 3678, L. 66; *3,4*, paratype, pedicle mold of the interior and rubber cast of same, F. 3679, L. 66; *5*, paratype, rubber cast of the brachial interior showing cardinalia and adductor muscle imprints, F. 3681, L. 66.

6–13—Leptagonia cf. *L. analoga* (Phillips). *6,7*, brachial mold of the interior and rubber cast of same, F. 3604, L. 66; *8*, brachial mold of the interior showing pallial markings, F. 3608, L. 66; *9,10*, pedicle mold of the interior and rubber cast of same, showing prominent spoon-shaped spondylium, F. 3605, L. 66; *11*, enlarged view of cardinal process and chilidium of specimen shown in fig. *8*, ×2.3, F. 3608, L. 66; *12*, rubber cast of brachial exterior, F. 3606, L. 66; pedicle mold of the interior showing pallial markings, F. 3607, L. 66.

14–19—Pustula abbotti larga, n. subsp. *14*, holotype, pedicle mold of the interior, F. 3714A, L. 146; *15*, paratype, pedicle mold of the interior, F. 3712A, L. 146; *16*, paratype, rubber cast of the brachial interior, F. 3716, L. 146; *17*, paratype, rubber cast of the brachial exterior showing the trilobed cardinal process and spines, F. 3715, L. 146; *18*, portion of a rubber cast of the pedicle exterior of the specimen shown in Fig. *15*, ×2.3 (median anterior portion of valve), *19*, enlarged portion of the rubber cast shown in fig. *17*, ×2.3 (median anterior portion of valve).

ber of minor septa. The major septa are flexed, ending freely axially, or continuing as curved septal lamellae to form part of the loose axial column. Minor septa are long, extending about one-half the length of the major septa. Septa are dilated in the tabularium, more so in the cardinal quadrants. In the extremely dilated septa can be seen calcite fibers converging peripherally towards the dark median lines of the septa at angles approximating 60°. At the periphery of the tabularium, deposition of sclerenchyme causes lateral contact of septa; this diminishes away from the cardinal septum, and septa are free laterally in the vicinity of the counter septum.

Insertion of septa is accelerated in the counter quadrants. The adult pattern shows 17 major septa in each of the counter quadrants and 14 in each of the cardinal quadrants.

The cardinal septum is rather long, extending about two-fifths the length of the major septa. Septa bounding the cardinal fossula gradually increase in length away from the cardinal septum. Maximum length is not reached until about the fifth septum on either side of the cardinal septum. The counter septum is longer than the major septa, and flexed more before continuing as a septal lamella into the axial column.

The dissepimentarium occupies an area about equal to that of the minor septa, but normally the septa protrude just axially from it. The dissepimentarium extends approximately one-half the length of the major septa. Dissepiments are quite regular and are of the curved concentric type, becoming more crowded axially. In vertical section, dissepiments are elongate and very steeply inclined.

The axial column is dibunophylloid, occupying less than one-third the width of the corallum. It consists of relatively few curved septal lamellae and broadly tent-shaped to rather broadly arched tabellae. Combination of horizontal and vertical elements forms a rather loosely packed axial structure.

The tabularium is clearly divisible into an outer and inner series of tabulae. Outer tabulae are few and incomplete, broadly arched toward the axial column. Tabellae of the axial column are much more numerous, and broadly tent-shaped to rather highly arched.

The cardinal fossula is long and open, having a gradual expansion axially.

Ontogeny.—In the smallest section of specimen F. 3425 (diameters 11.5 by 15 millimeters), the counter septum appears connected with the poorly defined median plate, but at diameters 15 by about 18 millimeters, they have become separated. At the latter stage, septa are dilated within the tabularium, particularly in the cardinal quadrants. Deposition of sclerenchyme causes lateral contact of septa at the outer edges of the tabularium. This part of the stereozone diminishes in strength towards the counter septum where it is quite narrow. Minor septa are short, only about one-fourth the length of the major septa. The dissepimentarium is narrow, and incomplete or absent in the counter quadrants where the corallum has been eroded prior to burial. The axial structure is elongate, poorly defined, and very loose, consisting of but very few skeletal elements. The axially expanded cardinal fossula is present at this stage.

As ontogeny progresses, various easily observable changes occur. The stereozone migrates axially with the increase in length of the minor septa (and corresponding widening of the disseptimentarium). At the periphery of the tabularium, the stereozone diminishes more and more towards the counter septum. In adult stages, the septa are no longer connected laterally in the area of the counter septum. The axial structure changes from an elongate to a subelliptical shape, and finally becomes subcircular. Septal lamellae and tabulae increase in number and the whole axial structure becomes more dense and distinct. Likewise, the median plate becomes stronger and longer. Tabellae of the axial column change pattern from flat, strongly tent-shaped structures to ones which are more highly arched.

Remarks.—This species is placed provisionally in the genus *Cyathoclisia*, as certain differences are apparent. Notably different is the loose axial column which is much less dense than is characteristic of the genus. Also, septal lamellae are more curved in the

present species. However, considerable variation occurs in the axial structure of the type species, as can be seen in Dingwall's pl. 3 (Dingwall, 1926). The writer prefers to adopt a conservative attitude, although it is realized that variation in the axial structure may, perhaps, be of more than specific importance. The specific name, *laxicolumnaris*, refers to the loose axial column.

Occurrence.—This species is at present known only from the fossiliferous mudstone below the "*Productus*" *barringtonensis* bed, from the upper part of the Lower Burindi group, south of Barrington, N. S. Wales; upper Tournaisian.

Phylum BRACHIOPODA Cuvier, 1802
Suborder DALMANELLOIDEA
Moore, 1952
Family RHIPIDOMELLIDAE
Schuchert, 1913, emend.
Schuchert & Cooper, 1932
Genus RHIPIDOMELLA Oehlert, 1890

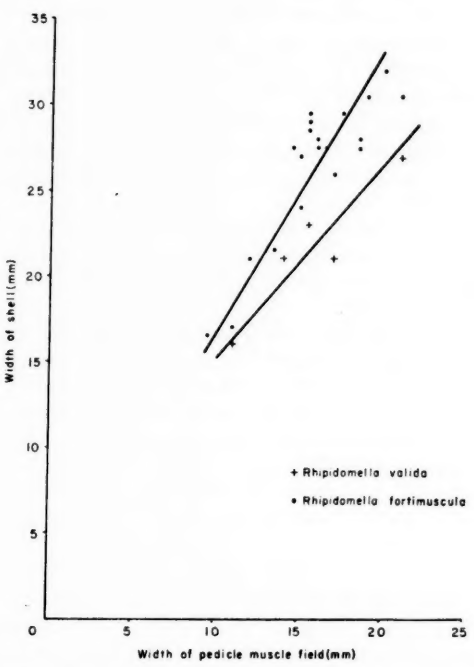
Type species.—*Terebratula michelini* L'Eveillé, 1835, Mém. Soc. Géol. France, v. 2, p. 39, pl. 2, figs. 14–17.

Diagnosis.—Unequally biconvex, the brachial valve the more convex; outline circular to subtrigonal; hinge line narrow; multicostellate; in pedicle valve, the semiflabellate diductor scars completely enclose the adductor scars; brachial muscle field quadripartite; large cardinal process of ponderous myophore supported by short shaft; blunt brachiophores, widely divergent.

Remarks.—It should be mentioned that Schuchert & Cooper (1932, p. 133), in their description of this genus, say that the posterior adductor scars of the brachial valve are the larger. Of the figures shown by by these authors, only fig. 20, pl. 20 can be said to have the posterior scars definitely larger. No species of *Rhipidomella* known to the writer have the posterior scars the larger. Relative size of brachial adductor scars does not appear to be a constant generic character.

RHIPIDOMELLA FORTIMUSCULA, n. sp.
Pl. 109, figs. 7–13; text-fig. 2

Diagnosis.—About medium-sized or larger for genus; shell subtrigonal, slightly wider than long; pedicle muscle field strongly impressed, separated by a rather broad ridge; costellae number about six to nine per 3 millimeters at the anterior margin of the shell.



TEXT-FIG. 2—Scatter diagram of width of shell /width of pedicle muscle field in *Rhipidomella valida* (Dun) and *R. fortimuscula*, n. sp. Specimens measured of *R. valida* (Dun) are topotypes.

Types.—Holotype, F. 3442, L. 66; paratypes, F. 3443-F. 3445A, and F. 3447, L. 66; University of New England Collections.

Material.—F. 3442-F. 3532, L. 66; University of New England Collections.

Description.—*Exterior:* Shell is slightly wider than long, with the greatest width at about the anterior one-third of the length; the lateral profile is moderately biconvex. The interarea is about two-fifths the width of the shell.

The pedicle valve is subtrigonal to almost subtrapezoidal; it is relatively flat near the anterior margin but becomes more convex posteriorly, and the umbo is somewhat inflated. At the anterior commissure is a very broadly defined shallow sulcus. The inter-

area is curved and rather strongly apsacline.

The brachial valve is slightly shorter, and subtrigonal to subcircular; the anterior commissure is broadly arched, with a shallow broad sulcus, extending from the beak to the anterior margin, superimposed on the fold. An essentially flat interarea is slightly anacline.

Both valves have numerous costellae, about 12 per 3 millimeters near the umbo and six to nine (per 3 millimeters) at the anterior margin.

Interior: The semiflabellate muscle field of the pedicle interior is deeply impressed, occupying about 50 to 64 percent the length of the shell. Diductor scars are impressed more posteriorly and rise gradually towards their anterior margin, which is broadly rounded to distinctly emarginate. Irregularly spaced longitudinal ridges are present within the anterior portions of the diductor field. A rather broad median ridge separates longitudinally the anterior half of the diductors and varies considerably in prominence and transverse profile. In transverse profile, it may be rather low with a bluntly pointed arch, or high with a flattened upper surface and straight sides.

The adductor scars (enclosed by the diductor field), commonly near the posterior end of the diductors, may be moved anteriorly to a sub-central position. They are impressed more posteriorly, rising gradually towards the anterior on a short platform; a pronounced ridge separates them laterally from the diductor scars. Commonly separating the heart-shaped adductor field is a small ridge; occasionally, however, no apparent separation is evident, although there is a low median fold.

A transverse rim borders anteriorly the pedicle callist, occasionally continuing up the inner side of the teeth. Also, a narrow median furrow extends the length of the callist and beyond to about the posterior end of the adductor scars. The teeth are prominent, bladed, and curved postero-laterally on their ventral edges; they point anterodorsally. Underlying the teeth, and commonly separated from them, are small and subdued dental lamellae, diverging at angles of 61 to 77°.

In the brachial interior, the anterior adductor scars are well impressed; the much smaller posterior adductor scars are on shelves and but faintly defined, commonly separated from the anterior scars by a transverse ridge. Brachiophores are prominent, diverging at angles of 75 to 85°. The cardinal process is prominent and quite erect, but directed slightly anteriorly; the myophore is trifid, appearing bluntly spear-shaped when viewed from the posterior. Ventrally from the plane of the interarea are buttress-like extensions supporting the myophore. The shaft of the cardinal process is thick and short, commonly partly obscured by adventitious shell material between it and the brachiophores. A rather low rounded median ridge extends anteriorly from the shaft, separating the adductor field.

The only pallial markings observed were two primary trunks, appearing as rounded depressions. Each trunk originates at the posterior portions of the anterior adductor scars; anterior extent of these markings is not known. Poorly defined pit-like depressions anterior to the adductor field are possibly ovarian markings. No pallial markings were seen on the pedicle valve, although feebly defined pit-like, possible ovarian markings were noted on some specimens.

Measurements.—(In millimeters)

Remarks.—Three other species of *Rhipidomella* have been described from the Lower Carboniferous of New South Wales; they are *R. valida* (Dun), *R. australis* (McCoy), and *R. myosa* Campbell. Topotypes were examined for all three species, and several distinguishing characters were noted, although only the more striking will be given here. Differences are stated with regard to *R. fortimuscula*, n. sp.

R. valida (Dun) differs in having (1) a less deeply impressed pedicle muscle field which is broader with respect to the width of the shell (see text-fig. 2), (2) a more anteriorly directed cardinal process, (3) a brachial muscle field which is more deeply impressed medially, and (4) less divergent brachiophores. Syntypes of this species, as well as topotypes, were examined for comparison with *R. fortimuscula*, n. sp. A lectotype is here designated from the suite of three syntypes. This specimen is housed at

Pedicle valves

Length of Shell	Width of Shell	Length of Muscle Field	Width of Muscle Field	Angle of Divergence of Dental Lamellae
ca. 34.5	ca. 32.0 (est.)	22.0	ca. 20.0 (est.)	75°
ca. 33.0	ca. 30.5	ca. 19.0	21.0	77°
ca. 28.0	ca. 30.5	ca. 18.0	19.0	76°
28.0	ca. 29.5	17.0	15.5	75°
27.5	29.5	17.5	17.5	65°
ca. 27.5	ca. 29.0	17.5	15.5	65°
27.5	27.5	15.5	14.5	68°
27.0	27.5	15.5	16.0	68°
ca. 26.5	27.5	16.0	16.5	64°
26.5	27.0	16.5	ca. 15.0 (est.)	—
ca. 26.5	ca. 26.0 (est.)	16.0	ca. 17.0 (est.)	—
ca. 26.0 (est.)	ca. 27.5	18.5	18.5	59°
ca. 25.5	ca. 28.5	18.0	15.5	66°
ca. 25.5	ca. 28.0 (est.)	ca. 15.0	18.5	ca. 79°
ca. 27.0 (est.)	ca. 28.0 (est.)	14.0	16.0	63°
23.5	24.0	14.5	15.0	77°
ca. 22.5	ca. 21.5	14.0	13.5	ca. 57°
20.5	22.5	11.5	13.5	69°
ca. 19.5 (est.)	ca. 21.0 (est.)	11.0	12.0	61°
18.5	17.0	11.5	11.0	71°
ca. 14.5	ca. 16.5	8.5	9.5	—

Brachial valves

Length of Shell	Width of Shell	Length of Muscle Field	Width of Muscle Field	Length of Anterior Scars	Average Width of Anterior Scars
ca. 33.0	ca. 34.0 (est.)	8.0	14.0	5.0	5.0
ca. 33.0	ca. 32.0	7.5	ca. 12.5	5.0	5.0
27.0	29.0	8.0	11.0	5.0	5.0
26.5	27.0	8.5	12.0	5.5	5.0
25.5	27.0	7.0	11.5	5.5	4.5
25.0	28.5	7.5	11.0	5.0	5.0
25.0	ca. 26.5	8.5	10.5	5.0	4.5
24.5	ca. 25.0	8.0	11.5	6.0	5.0
24.0	ca. 26.0 (est.)	8.5	12.0	6.0	5.5
ca. 24.0	ca. 25.0 (est.)	8.5	11.0	5.5	4.5
24.0	ca. 24.0	8.5	11.0	6.0	5.0
24.0	23.5	7.0	10.0	4.5	4.5
ca. 23.5 (est.)	ca. 27.0 (est.)	8.5	11.0	5.5	5.5
ca. 23.0	25.0	7.5	10.5	5.0	5.0
ca. 23.0	ca. 24.0	8.5	10.5	5.0	4.5
22.5	25.5	7.0	10.0	5.0	5.0
ca. 21.5 (est.)	ca. 21.0 (est.)	8.0	9.5	5.5	4.5
ca. 20.5 (est.)	ca. 22.5	9.0	13.0	6.0	6.0

the Australian Museum, Sydney, with the number F. 35603 (original number F. 3980, Mining Museum); it is figured in Dun (1904, pl. 60, figs. 2,2a) and is from the Lower Carboniferous at Rawdon Vale, Portion 9, Parish Knowla, County Gloucester.

R. australis (McCoy) has (1) less inflated valves, (2) less pronounced cardinalia, (3) a less impressed pedicle muscle field, and (4) a smaller brachial muscle field. *R. myosa* Campbell (1) is decidedly smaller, (2) has a less impressed pedicle muscle field, and (3) a broader median ridge in the brachial interior.

R. burlingtonensis (Hall) from the North American Osagean is similar but has its greatest width just anterior to the mid-length, a less impressed pedicle diductor field, and a less well-defined sulcus on the brachial valve.

R. fortimuscula, n. sp., appears to be most closely related to the type species.

Judging from figures of *R. michelini* (L'Eveille) in the works by Demanet (1934) and Davidson (1861), similarities are striking; however, some differences appear to be constant. For example, the pedicle muscle field of *R. fortimuscula*, n. sp. is more deeply impressed and the median ridge is broader.

The specific name is derived from the Latin *fortis* 'strong' and *musculus* 'muscle,' referring to the strongly impressed diductor field of the pedicle valve.

Occurrence.—To date, this species is known only from the fossiliferous mudstone below the "*Productus*" *barringtonensis* bed in the upper part of the Lower Burindi group, south of Barrington, N. S. Wales.

Suborder DALMANELLOIDEA
Moore, 1952
Superfamily DALMANELLACEA
Schuchert & Cooper, 1931
Family SCHIZOPHORIIDAE Schuchert & LeVene, 1929
Subfamily SCHIZOPHORIINAE Schuchert & LeVene, 1929
Genus SCHIZOPHORIA King, 1850

Type species.—*Conchyliolithus Anomites resupinatus* Martin, 1809, p. 12, pl. 49, figs. 13,14.

Diagnosis.—Shells resupinate, dorsal valve with greatest convexity; margins and cardinal extremities rounded; anterior commissure rectimarginate to uniplicate; multicostellate, test fibrous, punctate; pedicle interior with divergent or subparallel diductor scars separated by median septum bearing adductor scars; brachial interior with widely divergent brachiophores; anterior adductor scars separated from posterior ones by antero-laterally directed oblique ridges; four pallial trunks, originating as two and dividing, are present at the anterior extremity of median ridge; in some species, two trunks originate at end of ridge dividing adductors and pass antero-laterally (abstracted from Schuchert & Cooper, 1932, p. 143).

Remarks.—The type specimen of *S. resupinata* (Martin) has been lost, and in 1941, Bond (p. 289) designated a neotype. However, this was done before the neotype was recognized as a category of type specimen. In the 1948 meeting of the International Commission on Zoological Nomenclature, neotypes were recognized as valid. Provision 41 (see Hemming, 1953) provides for the reception of unofficial "neotypes," with certain requirements. Bond (written communication) informs the writer that the requirements for the designation of the neotype of *S. resupinata* has been fulfilled.

Schizophoria ranges from the Silurian to the Permian.

SCHIZOPHORIA VERULAMENSIS, n. sp.
Pl. 109, figs. 14–6; pl. 110, figs. 1–5

Diagnosis.—Shells about medium-sized for genus, hinge line approximating one-half width of shell; pedicle diductor field well impressed, especially medially; dental lamellae diverge at angles of about 71 to 87°; main pallial trunks originating at anterior ends of diductor scars, usually straight and subparallel, diverging slightly anteriorly; brachial adductor field well impressed; main pallial trunks, originating at anterior ends of posterior scars, diverging anteriorly; costellae number 10 to 12 per 3 millimeters at one centimeter from ventral umbo, and six to nine per 3 millimeters at anterior margin; shell structure very finely punctate.

Types.—Holotype, F. 3677A–B, L. 66; paratypes, F. 3678 and F. 3681, University of New England Collections.

Material.—F. 3677-F. 3711, University of New England Collections.

Description.—*Exterior:* Shells are about of medium size for the genus, and transversely subelliptical, the greatest width being at about the midlength. The hinge line averages about one-half the maximum width of the shell.

The pedicle valve is rather gently convex at the umbo, becoming slightly concave anteriorly. In transverse profile, the valve is slightly convex in the median portion, becoming gradually slightly concave on the lateral slopes. A shallow, broadly rounded sulcus is restricted to about the anterior one-half of the valve. The interarea is moderately high, slightly concave, and rather strongly apsacline. The delthyrium is open and triangular, slightly higher than wide. Costellae number about 10 to 12 per 3 millimeters at about 1 centimeter from the umbo, and about six to nine per 3 milli-

meters near the anterior margin. Costellae usually increase by intercalation; bifurcation may occasionally occur. Spine bases appear to be rather sparsely and randomly distributed over the surface of the shell.

The brachial valve is more strongly and rather uniformly convex, although its greatest convexity is at the umbo. In transverse profile, the valve is broadly arched and slopes rather rapidly toward the narrow, slightly concave areas on the lateral slopes. The interarea is slightly concave, considerably smaller than the pedicle interarea, and may be approximately orthocline to very slightly anacline. The notothyrium is widely triangular, and variably occupied by the cardinal process. The anterior commissure is broadly uniplicate, the fold being low and gently arched. A shallow, very poorly defined median sulcus, originating at or near the beak, is also present.

Interior: The diductor field of the pedicle valve is bilobate and subovate, extending approximately two-fifths the length of the valve. Anterior extremities of the field are bluntly pointed. Diductor scars are deeply impressed, especially medially along the median septum. A very short pedicle callist, ornamented with transverse growth lines, occupies the posterior tip of the delthyrial cavity. The prominent median septum, separating the diductor scars, varies in transverse profile from rather low and rounded to high and acute. Commonly, a shallow median groove extends less than one-half to nearly the length of the median septum. Adductor scars, along the flanks of the median septum, are not well-defined. Dental lamellae are short, diverging at angles of about 71 to 87°, and continuing as low ridges demarcating the diductor field. Teeth are rather prominent, subangular on their ventral surfaces, and bluntly pointed.

Two pallial trunks, appearing as flat-bottomed depressions, arise from the inner anterior ends of the diductor scars. These trunks are usually straight and subparallel, diverging but slightly toward the anterior margin. However, considerable variation may occur. They may be subparallel and converge anteriorly, or convex outward and converge anteriorly. Numerous secondary pallial markings are developed around and near the margin of the valve.

In the brachial valve, adductor muscle scars are similar to those described by George & Ponsford (1938, p. 244, and figs. 3a, p. 230) for *S. nuda* George & Ponsford. That is, the anterior scars are elongate and pyriform, the posterior scars bifid and digitate, with the innermost "finger" being the longer. In the present species, a posterior scar may be separated from an anterior scar by a low ridge, or there may be no apparent ridge, making differentiation of scars difficult. Medially separating the adductor field is a broad swelling which is bluntly spear-shaped, pointing posteriorly. This median swelling supports a narrow median ridge, which is suppressed posteriorly or merely represented by a longitudinal furrow. Two main pallial trunks, appearing in transverse section as flat-topped or broadly rounded ridges (in contrast to depressions in the pedicle valve), arise from the anterior ends of the anterior adductor scars. These trunks are rather straight, and diverge anteriorly. Two smaller trunks appear to arise from the inner ends of the anterior adductor scars or the median swelling, but their extent can not be determined with certainty. Commonly the main pallial trunks can be seen to extend posteriorly under the anterior scars, and the scars are seemingly "draped" over them. The cardinal process consists of a strong bilobed median process flanked on each side by about two to four narrow ridges, wider than the spaces between them.

Brachiophores (used in the sense of Schuchert & Cooper, 1932, p. 6) diverge at angles of about 75 to 83°. Brachiophore processes (at the distal end of the brachiophores) are knife-like and pointed, with bladed ventro-lateral edges, and are curved postero-laterally. Sockets are rather deep and rounded, supported by strong fulcral plates. Variable amounts of callus are deposited in the apical portions of the notothyrial cavity, at the base of the cardinal process, and on the innermost surfaces of the brachiophores. Puncta are exceedingly fine and numerous, usually .025 millimeter and less in diameter. The pedicle valve is also finely punctate, but puncta have not been suitably preserved to be measured.

Measurements.—(In millimeters)

Pedicle valves

Length	Width	Muscle field		Angle of divergence of dental lamellae
		Length	Width	
ca. 39	ca. 46 (est.)	15.5	11	83°
ca. 34 (est.)	44	ca. 16.5 (est.)	12	71°
ca. 33	ca. 34 (est.)	14	9	76°
ca. 31.5	36	14	10.5	87°
26.5	ca. 34	11.5	9	85°

Brachial valves

Length	Width	Muscle field		Angle of divergence of brachiophores
		Length	Width	
35.5	46.5	12.5	ca. 15.5	83°
33.5	ca. 44	10	13.5	75°
32	ca. 43.5	10	14	80°

Remarks.—In their discussion of *Schizophoria*, Schuchert & Cooper (1932, p. 143) say four pallial trunks originate at the anterior extremity of the median ridge in the brachial valve. The present species shows two main trunks originating at the anterior ends of the anterior adductor scar, and possibly two smaller trunks arising from the inner anterior ends of the scars or from the median ridge (swelling). Also, no pallial trunks, arising from the anterolaterally directed ridges separating anterior and posterior scars, have been observed.

S. sp. cf. *resupinata* from the upper Tournaisian of Babbinboon, N. S. Wales (Campbell, 1957, p. 48–51, pl. 12, figs. 1–5) differs in being slightly larger and having a wider hinge line. Also, pallial trunks of the pedicle valve converge anteriorly, instead of the usual divergence in the present species. Pedicle diductor impressions are slightly less impressed, especially medially. The brachial muscle field is less elongate and less deeply impressed; also, the median swelling is broader posteriorly and less prominent.

Specific characters of the type species

EXPLANATION OF PLATE 111

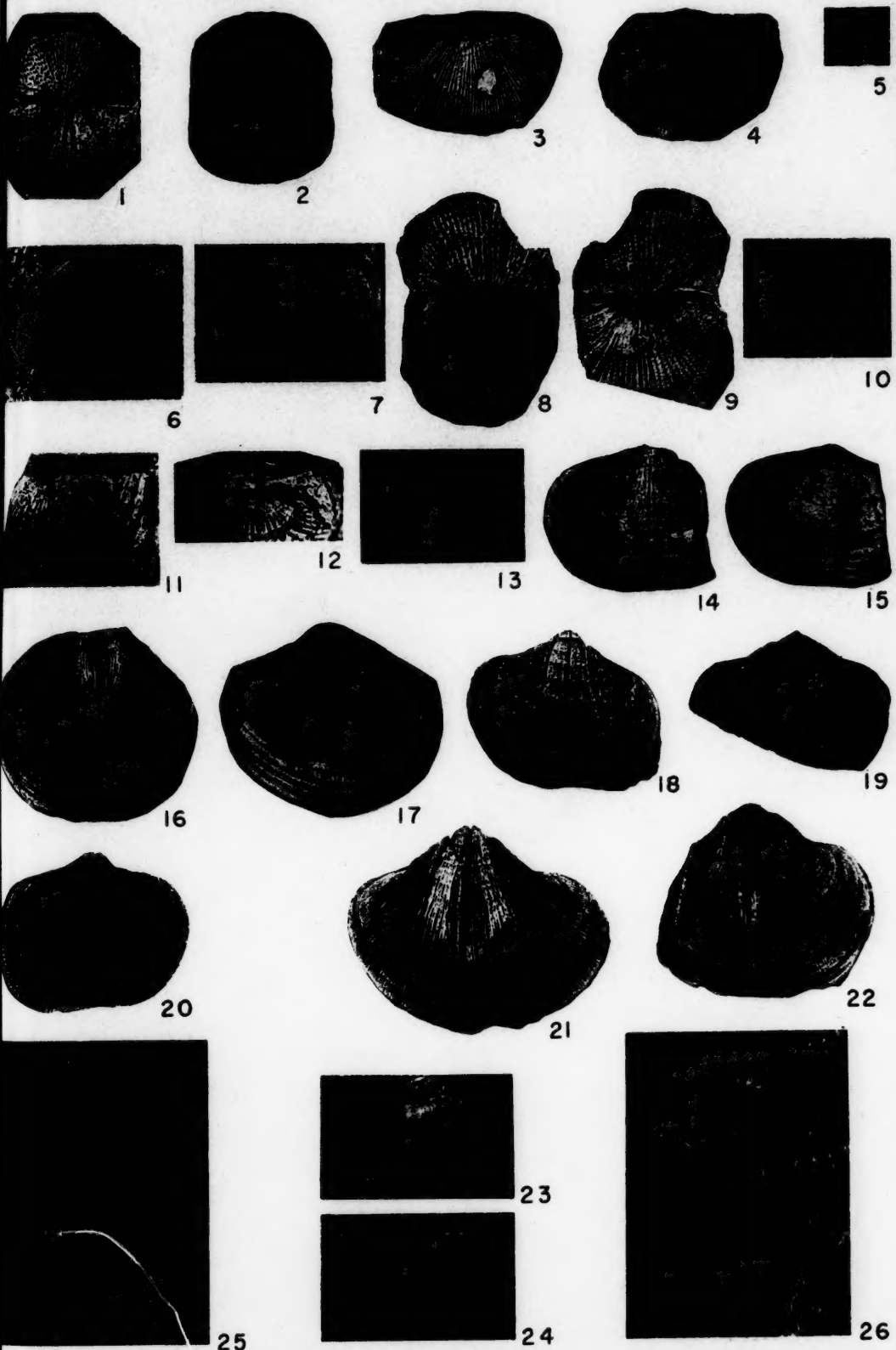
All figures are ×1 unless otherwise stated. Specimen F. numbers and collecting locality L. numbers are those of the University of New England.

FIGS. *1–7—Chonetes gloucesterensis*, n. sp. *1,2*, holotype, mold of the pedicle and brachial interiors, and rubber cast of same, respectively, ×1.9, F. 3809, L. 66; *3*, paratype, rubber cast of the brachial exterior, ×1.9, F. 3811, L. 66; *4*, paratype, rubber cast of the brachial exterior, ×1.9, F. 3813, L. 66; *5*, small median anterior portion of fig. *4* showing a few incomplete concentric lirae, ×11.5; *6*, paratype, pedicle mold of the interior, ×1.9, F. 3810, L. 66; *7*, paratype, pedicle mold of the interior, ×1.9, F. 3812, L. 66.

8–13—Plicochonetes sexfidus, n. sp. *8,9*, holotype, mold of the pedicle and brachial interiors, and rubber cast of the same, respectively, ×1.9, F. 3764, L. 66; *10*, paratype, mold of the brachial exterior, ×1.9, F. 3765, L. 66; *11*, paratype, mold of the brachial exterior, F. 3767, L. 66; *12*, portion of the brachial exterior and the cardinal process, ×2.3, F. 3769, L. 66; *13*, cardinal process of that specimen shown in fig. *12*, ×7.

14–20,23,25—Phricodothyris campbelli, n. sp. *14,15*, holotype, mold of the brachial interior, F. 1339A, and rubber cast of the brachial exterior, F. 1339B, L. 66; *16,17*, paratype, mold of the pedicle interior, F. 3724B, and rubber cast of the exterior, F. 3724A, L. 66; *18*, paratype, mold of the pedicle interior, F. 3725, L. 66; *19*, paratype, mold of the pedicle interior, F. 3726, L. 66; *20*, paratype, mold of the brachial interior, F. 3733, L. 146; *23*, median anterior portion of the specimen shown in fig. *17*, ×2.3; *25*, biramous spine bases from the left lateral slope of the specimen shown in fig. *15*, ×11.5.

21,22,24,26—Phricodothyris sp. *21,22*, molds of the pedicle interior, F. 3743 and F. 3745, respectively, L. 66; *24*, rubber cast of the median anterior portion of the pedicle exterior, ×2.3, F. 3749A, L. 66; *26*, biramous spine bases at the approximate middle of the sulcus and anterior to the midlength of the valve which is partially shown in fig. *24*, ×11.5.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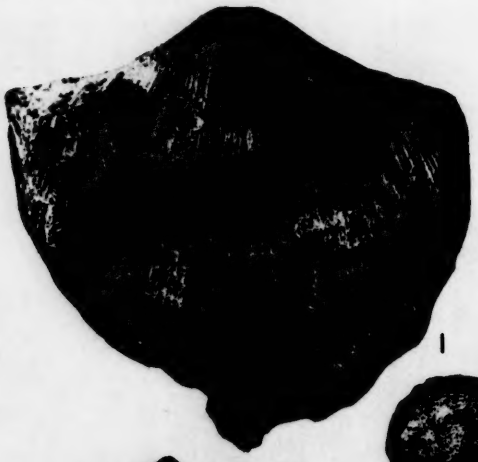
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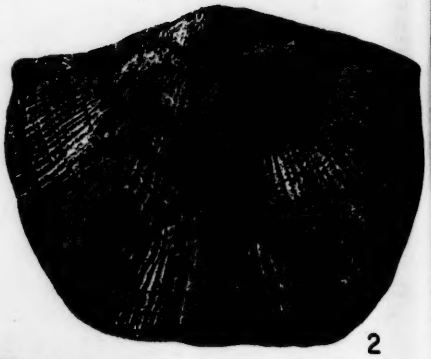
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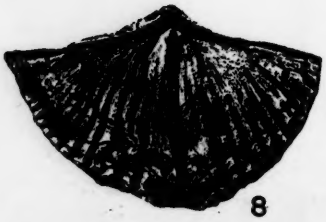
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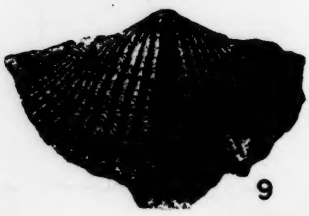
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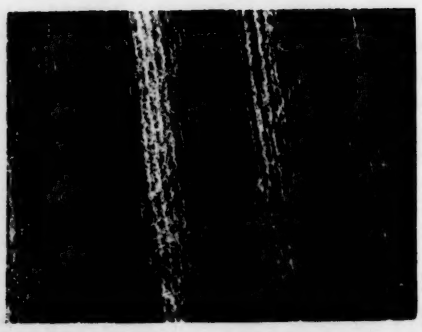
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were gained largely from Davidson (1861, p. 130–131), Bond (1941, p. 290; pl. 21, figs. A,B,C), and Demanet (1934). Although internal features of the neotype are practically unknown, differences between this and the present species, can be established. *S. resupinata* is generally larger, has a wider hinge line, and a better developed median sulcus on the brachial valve. The pedicle diductor field appears less deeply impressed and diductor scars are separated by a narrower median septum.

S. swallovi (Hall) (Weller, 1914) from the Burlington limestone (Osagean) of America is quite remarkably similar. However, it differs in having a slightly shallower median sulcus in the pedicle valve, and a more extensive pedicle diductor field, which may extend anteriorly beyond the middle of the valve.

Of the varieties of *S. resupinata* figured by Demanet (1934), *S. r.* var. *rotundata* appears to have the closer resemblances, especially in the deeply impressed pedicle diductor scars and the pattern of the ventral pallial trunks. This variety occurs in the upper Tournaisian (middle part of C_1, equivalent to Tn3b) and the lowermost Viséan (C_2, equivalent to V_1) of Belgium.

The specific name, *verulamensis*, is derived from the Parish of Verulam, in which the area of the present study is situated.

Occurrence.—At present, this species is known only from the fossiliferous mudstone below the *"Productus" barringtonensis* bed from the upper part of the Lower Burindi group, south of Barrington, N. S. Wales; upper Tournaisian.

Suborder STROPHOMENOIDEA Maillieux, 1932
Superfamily STROPHOMENACEA Schuchert, 1896
Family STROPHOMENIDAE King, 1846
Subfamily STROPHOMENINAE Gill, 1871, emend. A. Williams, 1953
Genus LEPTAGONIA McCoy, 1844

Type species.—*Producta analoga* Phillips, John, 1836, Geol. Yorkshire, pt. 2, p. 215, pl. 7, fig. 10.

Diagnosis.—Like *Leptaena*, but pedicle interior with well-developed spondylium, on which rests a strong, adductor platform; brachial interior with high, marginal ridge.

Remarks.—Sokolskaya (in Sarycheva & Sokolskaya, 1952, p. 35–36) erected the genus *Leptaenella* for those Leptaena-like forms having *Producta analoga* Phillips as their type species. This generic name has to be abandoned, however, since *Leptaenella* is an objective synonym of *Leptagonia*.

Campbell (1957, p. 40–41) discusses the differences between Leptaenas from the Lower Paleozoic and the Carboniferous. That is, mainly, a well-developed spondylium and a high internal brachial marginal ridge is present in Carboniferous forms, and a weak pseudospondylium and lower bra-

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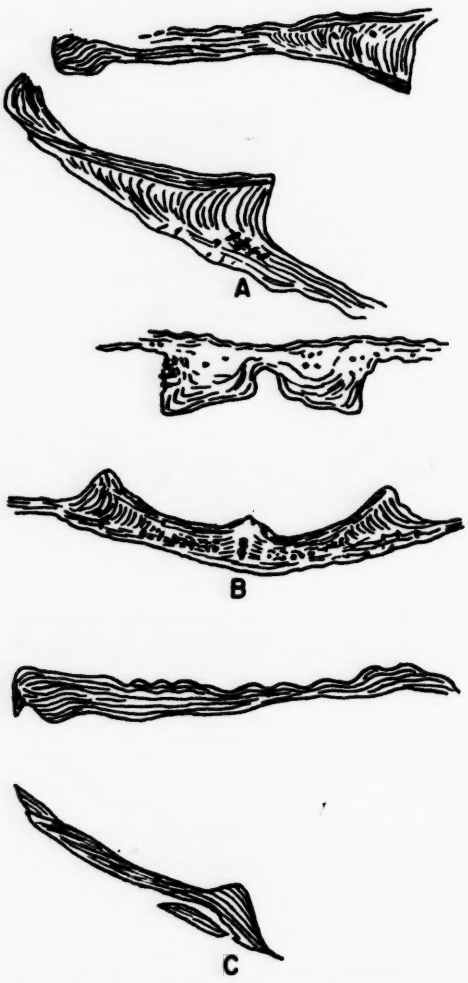
EXPLANATION OF PLATE 112

All figures are ×1 unless otherwise stated. Specimen F. numbers and collecting locality L. numbers are those of the University of New England.

FIGS. *1–7,11*—*Spirifer lirellus*, n. sp. *1*, holotype, incomplete pedicle valve, F. 3611A, L. 66; *2*, paratype, rubber cast of the brachial exterior, F. 3611A, L. 66; *2*, paratype, rubber cast of the brachial exterior, F. 3613, L. 66; *3*, paratype, mold of the brachial interior, F. 3614, L. 146; *4*, paratype, rubber cast of the pedicle interior, F. 3616, L. 66; *5*, negative print of a thin section cut normal to the commissure through the umbo; note the cardinal process, adventitious shell material on the inner surfaces of the dental lamellae, and the orientation of calcite fibers adjacent to the hinge line; ×2, F. 3617, L. 66; *6*, paratype, rubber cast of the umbonal interior, F. 3615, L. 66; *7*, right portion of fig. *6* showing hinge denticles, ×2.3; *11*, paratype, portion of a rubber cast of the pedicle exterior, showing radial lirae and occasional growth lines, at the approximate midlength of the valve on the right flank of the sulcus, ×11.5, F. 3612B, L. 66.

8–10,12—*Tylothyris planimedia*, n. sp. *8,9*, holotype, pedicle mold of the interior, F. 3391A, and rubber cast of the exterior, F. 3391B, L. 146; *10*, paratype, rubber cast of the pedicle exterior, F. 3392C, L. 146; *12*, median anterior portion of fig. *10* showing the gridlike microornament, ×11.5.



TEXT-FIG. 3—Longitudinal (A) and transverse (B) sections (×1) through the apical portions of *Leptagonia* sp. cf. *L. analoga* (Phillips) from the Carboniferous limestone of England. Fig. 3A from Bolland, Yorkshire shows a well-developed spondylium; fig. 3B from ?Little Island, Cork, Eire, shows a well-developed spondylium and adductor muscle platform. Fig. 3C is a longitudinal section (×1) through the apical portion of *Leptaena rhomboidalis* (Wilckens) from the Silurian Wenlock Limestone at Dudley, Worcestershire. This species has only a thickened diductor platform. In all sections, the brachial valve is uppermost.

chial ridge in Lower Paleozoic species. It is shown that there are two distinct leptaenid stocks.

The present work confirms those observations made by Sokolskaya and subsequently noted by Campbell. Thin sections were made of English Silurian specimens of *Leptaena rhomboidalis* (Wilckens) and Lower Carboniferous specimens of *Leptagonia* sp. cf. *L. analoga*. The Silurian material is from the Wenlock Limestone at Dudley, Worcestershire; Lower Carboniferous specimens are from the Carboniferous Limestone at Bolland, Yorkshire and at ?Little Island, Cork, Eire. Text-fig. 3 shows the Carboniferous forms to have a well-developed spondylium, and the Silurian species with only a somewhat thickened diductor platform or pseudospondylium. Text-fig. 4 shows the spondylium of *L.* sp. cf. *L. analoga* of this study to be stronger, but similar to that of the English Lower Carboniferous species.

LEPTAGONIA sp. cf. L. ANALOGA (Phillips)
Pl. 110, figs. 6–13; text-figs. 3, 4

Material.—F. 3587–F. 3610; University of New England Collections.

Description.—Exterior: Shells are subtrapezoidal, with the greatest width at the hinge line. The hinge line is essentially straight, but each side slants slightly anteriorly. Cardinal extremities are subauriculate.

The pedicle valve is slightly inflated at the umbo, becoming very slightly and broadly concave before bending sharply dorsally at the anterior margin. The interarea, anteriorly, is straight and flat, and rather strongly apsacline; posteriorly, it becomes curved and concave. A circular foramen is impressed on the umbo, and separated from the interarea, as in the epithyrid position of Thomson (1927, p. 72, fig. 20e). The foramen appears to be lined with a tubular sheath.

The brachial valve is flat or depressed on the umbo, and almost flat or slightly convex at about the posterior one-half of the length; anteriorly, it becomes more strongly convex, sloping into the marginal furrow. At the point of geniculation, the anterior flange of the shell bends sharply dorsally. A much shorter anacline interarea is concave postero-ventrally.

Surface sculpture is both radial and con-

centric. Radial costae number about seven to nine per 5 millimeters at the antero-median margin of the marginal furrow. Costae bifurcate and intercalate; anterior to the marginal furrow, they become finer gradually, with more frequent bifurcations and intercalations. Concentric sculpture is of rugae and very fine fila. Rugae are irregularly spaced, and number about 16 to 20; they become coarser and higher on the posterolateral slopes, where they give the shell surface a more wrinkled effect. Fila (raised concentric threads) are extremely fine (about 24 per millimeter), distinctly crossing both costae and intervening furrows.

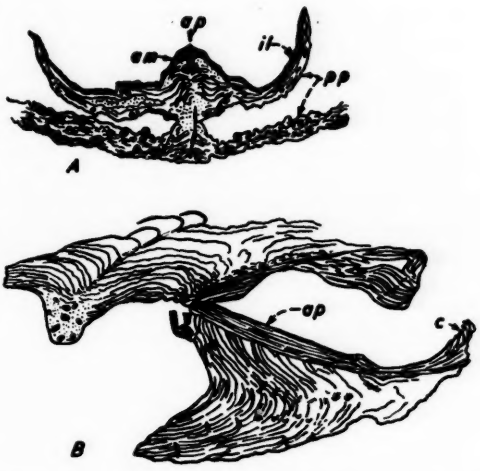
Interior: The most conspicuous structure in the pedicle valve is the spondylium. Its margin thins to a sharp ridge, curving postero-ventrally. Anteriorly, this structure is supported on a median thickened ridge, but becomes fused with the floor of the valve posteriorly (see text-fig. 4).

An adductor platform, triangular in transverse section, divides the spondylium medially. This platform originates some distance anterior to the apex (*i.e.*, superficially; in thin section it can be seen to continue apically as a thin extension, see text-fig. 4B), gradually thickening anteriorly, and extending to the tip of the spondylium.

The diductor muscle field is flabellate, and divided into two lobes by the adductor platform. Muscle scars begin posteriorly, at about the position where the adductor seemingly originates, and continue to the anterior end of the spondylium. Adductor scars are narrow, elongate scars on the flanks of the adductor platform, and are separated by a sharp, median ridge.

Teeth are widely divergent, almost subparallel to the hinge line. On the anterior portion of the delthyrium, these structures are rather thin, but end antero-laterally in thickened lobes. Posterior surfaces are flat, and anterior surfaces rounded; all contacting surfaces are covered with ridges and finer grooves. Posteriorly and anteriorly the the teeth are bounded by narrow grooves, corresponding in position to narrow socket-bounding ridges of the opposite valve.

The delthyrium is widely triangular, and practically filled by the large cardinal process. In the apex of this opening, is a short, arched deltidium (see discussion of this under remarks). Anteriorly bounding the deltidium, and resting on the apical floor of the spondylium is a short, thickened structure or callist (see text-fig. 4B). This callist is sharply bounded by a transverse ridge, and covered with numerous, sharp irregularly spaced, transverse growth lamellae. Arber (1939, p. 83) proposed the name secondary pseudodeltidium for this structure, and says it is commonly associated with a pedicle lost at an early stage, or with one which migrated anteriorly.



TEXT-FIG. 4—Transverse (A) and longitudinal (B) sections (×4.4) through the apical portions of *Leptagonia* sp. cf. *L. analoga* (Phillips) from the Lower Carboniferous near Gloucester, New South Wales. Fig. 3A shows a well-developed spondylium and adductor platform; fig. 3B shows the spondylium overlain by the adductor platform of the brachial valve; *am*=adductor muscle impression, *ap*=adductor platform, *c*=callist, *il*=impunctate lamellar shell, *pp*=pseudopunctate shell.

Taleolae (internal calcitic rods, terminology of Williams, 1956, p. 251–252) appear confined to two broadly suboval lobes, antero-lateral to the spondylium. Taleolae appear coarser adjacent to the spondylium, becoming finer and more oblique antero-laterally.

Medially, pallial markings begin as two linear primary trunks at the anterior edge of the spondylium. These trunks, represented as rounded ridges, are separated by

a narrow furrow, which, in itself, contains a thin ridge. At about the length of the supposed anterior margins of the pseudopunctate areas, are numerous fine, frequently bifurcating pallial markings; they extend marginally around the pseudopunctate areas. These fine markings appear as narrow ridges with impressed margins; occasionally, ridges are not clearly discernible and markings themselves appear as narrow grooves.

In the brachial interior, adductor scars are on a thick muscle platform, which is triangular in shape, tapering anteriorly. Posterior scars are irregularly quadrilateral and deeply impressed, more so posteriorly and medially, gradually extending ventrally on the antero-lateral margins. These scars are bounded antero-laterally by limiting ridges of the platform, postero-laterally by ridges anterior to the sockets, and posteriorly by ridges extending from bases of the cardinal process. These latter ridges converge and fuse at about mid-length of the posterior adductors, occasionally forming a narrow boss or ridge at the point of fusion.

The small anterior adductor scars are elongate, teardrop-shaped and divergent, bounded postero-laterally (and partially enclosed by) the posterior scars. A slight ridge separates these small scars from the posterior ones, but it is not seen on all specimens. These anterior scars appear as eminences, gradually extending ventrally as do the posterior scars.

Lying between the divergent anterior adductors, is a very deeply impressed spoon-like depression with straight, diverging lateral margins. Two anteriorly converging ridges bound the anterior margin of this depression, and unite near the position of the anterior tips of the anterior scars. At the point of fusion is formed a sharp, median ridge, which begins convexly and continues broadly concavely, gradually curving ventrally before ending in a point. This sharp ridge separates a concave, sub-triangular to cordate depression, which is bordered laterally by thick ridges, anterior extensions of the muscle platform.

The bipartite cardinal process is oriented at right angles to the plane of the valve, or directed somewhat posteriorly. The lobes are rather narrow, curved platelike structures, hollowed out or concave anteriorly, and convex posteriorly. The extreme posterior edges of the lobes appear almost flat (although broadly curved) and are covered with numerous very fine sinnuous striae, marking the position for the anchorage of the diductor muscles. A chilidium curves around the cardinal process, extending about one-half the height of this structure.

A narrowly triangular (widening ventrally) rounded furrow occupies a median position on the chilidium. Between the platelike lobes of the cardinal process lies a hollowed out, broadly rounded basin-like depression.

Sockets are well-defined and bounded by two thin ridges which become thickened on their lateral ends. One ridge is along, and almost parallel to, the hinge line; the other is along the posterior edge of a prominent ridge which bounds the posterior edge of the adductor scars. The walls of the sockets have ridges and furrows, corresponding to those on the contacting surfaces of the teeth.

The conspicuous marginal ridge is high and sharp, roughly following the contour of the valve except postero-laterally. Here each side of the ridge curves inward, and gradually diminishes in height, evanescing before reaching the interarea.

Taleolae appear mainly restricted to two suboval areas on each side of the muscle platform; however, the subtriangular to cordate depression anterior to the anterior muscle scars also appear pseudopunctate. Taleolae appear coarser adjacent to the muscle platform, becoming finer and more oblique, laterally and anteriorly.

Pallial markings are fine, narrow, rounded fingerlike ridges, with their margins impressed into the shell. Primary trunks begin at the anterior portion of the muscle platform; laterally, the pallial markings begin at the supposed margins of the pseudopunctate areas. These pallial ridges, bifurcating frequently, continue unbroken over the marginal ridge, and terminate just before reaching the margins of the shell.

Remarks.—Cloud (1942, p. 18–20) gives a good discussion of the confusion in the use of deltidium and pseudodeltidium, proposed by Von Buch (1835) and Bronn (1862), respectively. Both terms, as originally pro-

posed, are difficult to apply since several interpretations can be made of each. As a result, the two terms have been used inconsistently and generally oppositely by European and North American workers.

After consideration of the matter, the writer prefers to accept one of Cloud's suggestions and adopt deltidium as a nongenetic general term, but use deltidium for a single plate and deltidial plates for component parts. As suggested, suitable adjectives, such as fused, conjunct and discrete, could be used for description of the component parts. The term pseudodeltidium could be dropped, since it is ambiguous, awkward, and is lacking in priority.

It is realized that in certain brachiopods (members of the genus *Lacazella*), a primary structure is formed in the embryo for the covering of the delthyrium. It is appropriate athat a different term be applied for this primary plate; in fact, Cloud (1942, p. 20) proposed the term xenidium for the delthyrial covering in the strophomenoids. Now whether *Leptaena*, and other strophomenoids, have a primary, embryonic delthyrial plate is a doubtful point. This has been suggested (Arber, 1939, 1942), but no conclusive proof has been made. The recent genus *Lacazella* (which has the primary plate) belongs to the family Thecideidae, which has but a doubtful affiliation with the Strophomenacea (Thomson, 1927, p. 139).

Much consideration has been given as to whether the species studied should be comparatively referred to *L. analoga*, or a new name erected for it. One would expect at first thought, for Australian and British species to be very different, for although both species are from similar horizons, they are greatly separated areally. The writer was not able to examine type specimens or study the original figure or description. The latter condition, however, can possibly be left undone with clear conscience, for Weller (1914, p. 49) says, " . . . it is not possible to determine from Phillip's original description and figure just what the essential characters of the species are."

Be that as it may, a fair idea of the specific characters of *L. analoga* was gained by a study of published literature, especially the figures of Davidson (1861, pl. 28, figs. 1–6; 9–13) and Demanet (1934, pl. 5, figs. 1–14). After a close comparison, no noteworthy differences could be found between the species under discussion and *L. analoga*. The writer's specimens differed only in having somewhat coarser radial ornament and possibly less pronounced rugae. Internal characters appeared very similar in both species.

Other specimens from New South Wales referred to *L. analoga* Phillips have been examined from Babbinboon, Clarencetown, and Hilldale, all localities in the Lower Burindi group of the Lower Carboniferous. All species from the three above localities show useful differences. They differ from the species under consideration in having, (1) a more transverse spondylium, (2) finer radial ornament, and (3) a less transversely subtrapezoidal shape. In addition, specimens from Babbinboon are larger, and have a less acute pedicle adductor platform; Clarencetown specimens may also become larger, and have a less acute adductor platform in the pedicle valve; Hilldale specimens have a larger, more ponderous brachial muscle platform.

In America, *L. analoga* (Phillips) is represented in the late Kinderhookian and early Osagean, both series being equivalent to the Tournaisian of Europe. In Belgium (see Demanet, 1934, p. 104), *L. analoga* ranges through most of the Dinantian, from the Tn2a(Z_1) to V3b(D_3) zones. In the Bristol area of Britain, *L. analoga* is abundant in the K and Z zones, but unknown in C.

Muir-Wood (1948, p. 59) discusses the occurrence of *L. analoga* in the Tournaisian and Viséan of Asia.

Occurrence.—This species was collected from the fossiliferous mudstone below the "*Productus*" *barringtonensis* bed from the upper part of the Lower Burindi group, south of Barrington, N. S. Wales; upper Tournaisian.

Suborder PRODUCTOIDEA
Maillieux, 1940
Superfamily PRODUCTACEA
Waagen, 1883
Family ECHINOCONCHIDAE Stehli, 1954
Genus PUSTULA Thomas, 1914

Type species.—*Producta pustulosa* Phillips, John, 1836, Geol. Yorkshire, pt. 2, p. 216, pl. 7, fig. 15.

Diagnosis.—Pedicle valve convex, brachial valve flat or gently concave, moderately deep visceral cavity; geniculate or nongeniculate; both valves ornamented with oblique spines of same rank or size occurring in one row on concentric bands; each higher at anterior margin than posterior part of next succeeding one; bands increase in width from beak to anterior margin (Sutton, 1938, p. 554).

Remarks.—Campbell (1956, p. 476) discusses the occurrence of this genus in England, Germany and America. *Pustula* occurs through most of the Avonian in England and extends into the Pennsylvanian in America.

PUSTULA ABBOTTI LARGA, n. subsp.
Pl. 110, figs. 14–19

Diagnosis.—Large *P. abbotti* with pronounced brachial muscle field.

Types.—Holotype, F. 3714, L. 146; paratypes, F. 3712 and F. 3715–F. 3716, University of New England Collections.

Material.—F. 3712–F. 3723, University of New England Collections.

Description.—Exterior: Shells are about of medium size for the genus, and nongeniculate. The pedicle valve is moderately convex, having its greatest convexity near the umbo. Cardinal extremities are short, somewhat rounded to obtusely subangular, and slightly turned ventrally. A shallow sulcus, very obtusely subangular to rounded, extends from the beak to the anterior margin. The surface is covered with concentric bands which become crowded together on the lateral slopes. Bands number about four to seven per 10 millimeters on the median anterior portion of the valve. Spine bases are arranged in irregular rows on the concentric bands and have a density of about nine to twelve per 5 millimeters on the median anterior portion of the valve. Long fine spines are concentrated on the short auriculations.

The brachial valve is slightly concave with a broad rounded fold that arises just anterior to the umbonal area. On the median portion of the umbonal area, is a subtriangular concave region, diverging anteriorly. Auriculations are poorly defined, and slightly turned ventrally. Concentric bands are somewhat more numerous than on the pedicle valve, numbering about eight per 10 millimeters on the median anterior portion of the valve; they also become crowded on the lateral slopes. Spine bases vary in density from eight to eighteen per 5 mm. on the median anterior portion of the valve. Spine bases, arranged in irregular rows on the concentric bands, are especially numerous in a rather wide region near the margin of the valve. Spines are occasionally preserved in patches as long fine projections, almost hair-like in appearance.

Interior: In the pedicle valve, the flabellate diductor field extends approximately one-fourth the length of the valve. On the surface of each diductor scar are narrow longitudinal striated areas separated by much narrower rounded ridges. Adductor scars are narrow low rounded ridges between the diductor scars, their anterior margins about even with that of the diductor field, or slightly forward. Adductor scars appear to be divisible into two sets, the larger set having its surface covered with dendritic ridges. The smaller set is limited to two small subelliptical, relatively smooth areas on the extreme anterior portion of the adductor field. These smaller scars are poorly defined from the larger scars. A narrow furrow, which may have included a narrow ridge, widens anteriorly, and separates medially the two adductor scars. The interior surface is covered by shallow concentric rounded furrows, corresponding to external concentric bands. Shallow radiating depressions, corresponding to spine bases, are also present.

In the brachial valve, a median ridge extends about three-fifths the length of the valve, and separates a set of prominent, elongate adductor scars. The median ridge is narrowly rounded about the posterior one-half of its length, and then becomes sharp and thin, reaching its maximum height just anterior to the ends of the adductor scars, before disappearing rather gradually. Adductor scars are on a raised platform which extends about two-fifths the length of the valve. These scars are divisible into two

sets similar to those on the pedicle valve. Posterior scars are very elongate, expanding gradually anteriorly, and ornamented with coarse dendritic ridges. Anterior scars are short, smooth, semielliptical impressions at the extreme anterior end of the adductor field, and partially enclosed by the posterior scars. These anterior scars are better defined than those on the pedicle valve; their surfaces are slanted medially toward the median ridge.

Narrowly rounded ridges, which become flattened laterally, extend along the hinge line from the base of the cardinal process. The strong cardinal process is oriented somewhat postero-dorsally. Its postero-ventral surface is bifid, and its dorsal surface trifid; each lobe is ornamented with several lamellae.

Numerous taleolae are arranged in irregular rows along concentric areas corresponding in position to external concentric bands. These taleolae are directed anteriorly and laterally at low oblique angle, being more pronounced in the median anterior portion of the valve.

Measurements.—(in millimeters)

Pedicle valves

Length	Width
ca. 40	ca. 42 (est.)
ca. 39	ca. 46
ca. 35	ca. 40 (est.)

Brachial valves

Length	Width	Length of Median Septum	Length of Adductor Field	Width of Adductor Field
49.5	ca. 70	—	—	—
47	ca. 64	—	—	—
34	ca. 41	21	14	8
32	42	—	—	—
25.5	34.5	—	—	—

Remarks.—In addition to being larger and having a more pronounced brachial muscle field, there are other observable differences of this subspecies from *P. abbotti* Campbell P. abotti has a cardinal process which is directed more antero-dorsally, and the brachial adductor area is different. Its adductor scars diverge anteriorly away from the median ridge. In *P. a. larga*, the adductor scars adjoin the median ridge throughout their extent. There are very possibly other differences, but lack of complete type material of *P. abotti* makes further evaluation uncertain.

P. abbotti Campbell (1956, p. 476–477) has its type locality west of Stroud, N. S. Wales, and its stratigraphic position is uncertain, though probably upper Tournaisian.

It is possible that further study of complete specimens of *P. abbotti* will necessitate *P. a. larga* be given specific status. This move would be supported, if the stratigraphic positions of these two forms are found to be different.

The writer is not aware of any foreign species closely comparable with the present subspecies. However, there are certain resemblances with *P. pilosa* Thomas (1914, p. 284–286, pl. 20, figs. 3,4) from the Carboniferous Limestone of Little Island, Ireland.

The subspecific name, *larga*, is derived from the Latin *largus* 'large,' referring to the large size of the subspecies.

Occurrence.—At present, this subspecies is known only from the fossiliferous mudstone below the "*Productus*" *barringtonensis* bed from the upper part of the Lower Burindi group, south of Barrington, N. S. Wales; upper Tournaisian.

Suborder CHONETOIDEA
Muir-Wood, 1955
Superfamily CHONETACEA Shrock & Twenhofel, 1953
Family CHONETIDAE Waagen, 1884

Subfamily CHONETINAE Waagen, 1884
Genus CHONETES Fischer de Waldheim, 1830–1837

Type Species.—By subsequent designation of de Verneuil (1845), *Terebratulites sarcinulatus* Schlotheim, E. F. Von, 1820, Die Petrefactenkunde auf ihrem jetzigen Standpunkte . . . , p. 256, pl. 29, fig. 3.

Diagnosis.—Concavo-convex; pedicle valve with low but rather well-defined median septum extending beyond the midlength of the valve; brachial valve with long median ridge flanked by short diverging ridges, which separate the adductor scars; cardinal process quadripartite; multicostellate.

Remarks.—Much confusion has resulted with regard to what should be the type species of this genus. Ramsbottom (1952, p. 11) discusses this and shows clearly that *Terebratulites sarcinulatus* Schlotheim is the type species. However, although the type species is now correctly established, its characters are not clearly defined, Schlotheim's description and illustrations are inadequate for proper definition of the species, and the location of type specimens is apparently unknown. Therefore, in order to gain an understanding of the type species, a study was made of specimens from the type locality. Topotypes came from Rammelsberg near Goslar in the Harz of Germany; these specimens are Lower Devonian in age (upper Emsian of the Coblenzian) and stratigraphically from the Festenburger shale of the Kondel group. The above diagnosis was erected on the basis of study of topotypic material.

CHONETES GLOUCESTERENSIS, n. sp.
Pl. 111, figs. 1–7

Diagnosis.—Shells small for genus, greatest width anterior to hinge line; slight constriction of lateral margins just anterior to hinge line and lateral margins meet hinge line at approximate right angles; intercalating costellae 20 to 23 per 5 millimeters at anterior margin of shell; surface covered with numerous, fine concentric lirae.

Types.—Holotype, F. 3809, L. 66; paratypes, F. 3810–3814, L. 66, and F. 3815–3816, L. 145; University of New England Collections.

Material.—F. 3809–F. 3836, L. 66 and L. 145; University of New England Collections.

Description.—*Exterior:* Shells are subsemicircular to subrectangular, with the greatest width anterior to the hinge line, just posterior to the midlength. The average length of the shell is two-thirds that of the width. Lateral margins meet the hinge line at approximately right angles. Immediately anterior to the hinge line, the lateral margins constrict slightly, and then expand slightly, to form the maximum width of the shell. Cardinal extremities are essentially flat, but may be slightly turned ventrally.

The pedicle exterior is imperfectly known, but a reasonably accurate knowledge of the general profile can be gained from internal molds, since the shell is thin. In longitudinal profile, the valve has its greatest convexity at the umbo, and becomes gently convex anteriorly, and almost flat at the anterior margin. In transverse profile, the median portion of the valve is moderately to gently arched, sloping gradually toward the narrow lateral slopes. A partial very shallow median depression may be present, giving a slight wave to the anterior commissure. The interarea is slightly concave and slightly apsacline near the beak and almost flat and and moderately apsacline laterally. The delthyrium is broadly triangular, and almost entirely occupied by the cardinal process. Cardinal spines are imperfectly known, but are relatively few, possibly six to seven. They become larger and less inclined toward the beak laterally, similar to that shown by Dunbar & Condra (1932, p. 139, fig. 5) for *Chonetes graulifer* Owen.

The brachial valve is deeply concave immediately anterior to the hinge line, and becomes almost flat near the anterior margin. A very low broad fold may be present, corresponding to the shallow median depression occasionally found in the pedicle valve. The interarea is considerably shorter than that of the pedicle valve, and essentially flat. It is orthocline to slightly apsacline near the beak, and becomes moderately apsacline laterally. The notothyrium is closed by a short chilidium, which covers a portion of the fairly prominent cardinal process. The quadripartite cardinal process

consists of a longer median pair of lobes, flanked by a shorter lateral pair. Median lobes are separated by a deep, narrow furrow, and lateral lobes are separated from the median lobes by broader, rounded furrows.

The surface of the shell is covered with numerous costellae and very fine concentric lirae. Costellae number 20 to 23 per 5 millimeters at the anterior margin; they increase by intercalation, which occurs frequently and appears randomly distributed on all areas of the shell. Both costellae and intervening furrows are narrowly rounded in transverse profile. The width of the furrows varies most commonly from one-third to two-thirds the width of the costellae, depending upon the presence or absence or nearby intercalation. Abundant concentric lirae cover the entire surface of the shell, traversing both the costellae and intervening furrows. These lirae are quite regularly spaced, and number about 20 per one millimeter near the umbo, and become slightly more crowded at the cardinal extremities.

Interior: The pedicle valve has a rather poorly defined flabellate diductor muscle field, which extends about one-third the length of the valve. Each of the two lobes of the muscle field is separated from the median septum by a ridge and a furrow. The ridges, which may possibly be pallial trunks, appear to extend from the anterior ends of the two small teardrop-shaped adductor scars. These adductor scars are in the posterior end of the diductor field, extending slightly less than one-third the length of the field.

The median septum extends from greater than one-half to three-fifths the length of the valve. It begins at the interarea as a relatively high, sharp thin structure and diminishes fairly rapidly to the floor of the valve before reaching the end of the muscle field. It then rises again very gradually and extends in front of the muscle field margin as a low subdued structure. In longitudinal profile, the median septum begins posteriorly as broadly concave, and then broadly convex before diminishing to the floor of the valve.

Teeth are flat, short, and broadly rounded at their anterior ends. They are oriented subparallel to the hinge line.

Taleolae are radially arranged, each row in a position marking that of an external furrow. These structures appear subdued on the central portion of the valve, and more dominant marginally. They appear absent at the immediate margins, gradually diminishing in extent toward them. Taleolae appear largest and highest on the immediate lateral slopes, where they are oriented approximately normal to the plane of the valve. Around the margins, taleolae are inclined marginally.

In the brachial valve, a median ridge extends about two-fifths the length of the valve, and is flanked by two shorter diverging ridges. The lower, thinner, and sharper diverging ridges extend about one-eighth the length of the valve and diverge at about 50°. Muscle scars are poorly defined, and can not be differentiated with certainty. However, there appear to be two larger widely diverging posterior scars lateral to the diverging ridges, and two shorter teardrop-shaped anterior scars between the diverging ridges and the median ridge. Sockets are narrow, rather deep, and well-defined; they are widely divergent, approximately subparallel to the hinge line.

In contrast to that of the pedicle valve, teleolae appear more concentrated on the central area of the brachial valve, decreasing in size and extent laterally and anteriorly. No taleolae are visible on the posterolateral slopes.

Measurements.—(In millimeters; see next page).

Remarks.—This species resembles *Chonetes illinoisensis* Worthen as recorded by Weller (1914, p. 81–82, pl. 8, figs. 63–70) from the Burlington and Keokuk limestones (both Osagean) of the Mississippi Valley in the United States. The latter species differs in the more numerous costellae and perhaps the somewhat greater convexity of the pedicle valve.

Chonetes careyi Campbell (1957, p. 63–65, pl. 12, figs. 21–26) from the upper Tournaisian at Babbinboon, N. S. Wales, has finer costellae and a shorter median septum in the pedicle interior.

Occurrence.—At present, this species is known only from the fossiliferous mudstone

Pedicle valves

Length	Width	Width at Hinge Line	Length of Median Septum
11.5	16	ca. 14	8
ca. 11.5	14	13	—
10	15	14	ca. 6 (est.)
7.5	13	12	ca. 5
7	ca. 9.5	9	ca. 4
ca. 6.5	9.5	9	ca. 3

Brachial valves

Length	Width	Width at Hinge Line
11	16	15
10.5	ca. 15	ca. 14
10.5	14.5	13
ca. 10	ca. 15	ca. 14
9.5	ca. 16	ca. 14
9.5	ca. 15	ca. 14
9.5	14	14
9	ca. 14	ca. 13
8.5	ca. 12	ca. 11
8	12	ca. 11
8	11.5	10.5
7.5	12.5	11.5
7.5	12.5	Length of median ridge, 3
7	11	10.5
7	10.5	9.5

below the "*Productus*" *barringtonensis* bed from the upper part of the Lower Burindi group, south of Barrington, N. S. Wales; upper Tournaisian.

Genus Pliochonetes Paeckelmann, 1930

Type species.—*Chonetes buchiana* de Koninck, L. G., 1847, Recherches sur les Animaux Fossiles, pt. 1, Monographie des Genres *Productus* et *Chonetes*, p. 218, pl. 20, figs. 17a,b.

Diagnosis.—Small or rarely medium-sized chonetids with thin shells; surface of shells plicate.

Remarks.—It is unfortunate that this genus has been erected solely on external characters, for although these are often diagnostic, it is very important to have internal characters as well. The original description of the type species was consulted, but little pertinent knowledge could be gained from it. Only a single internal feature was mentioned; *i.e.*, the presence of a short median septum in the pedicle valve. With such a few characters available, it should be realized that the species below can only be assigned with some doubt to the genus *Plicochonetes*.

A question might be raised about certain features of the shell. Sokolskaya (1950, p. 23), in her description of *Rugosochonetes*, discusses characteristic transverse ridges ornamenting the radial "striae" (costellae) and giving the shell a wrinkled appearance. *Plicochonetes* is said by her to have the same characteristic ridges. It is assumed from her description that these transverse ridges are external.

In the specimens at hand, the transverse ridges are seen to be ***within*** the structure of the shell, and are only seen on exfoliated specimens. On well preserved specimens, plicae are smooth, except for irregularly spaced growth lines. Examination of pl. 10, fig. 15 (Sokolskaya, 1950) indicates the above observation to be true. Only that portion of the valve which is exfoliated shows strong transverse ridges on the plicae.

Rugosochonetes differs from *Plicochonetes* in having many thin costellae, averaging 100 to 150. *Pliochonetes* ranges from the Devonian to the Upper Carboniferous.

Plicochonetes sexfidus, n.sp. Pl. 111, figs. 8–13

Diagnosis.—Shells about medium-sized for genus, with greatest width at hinge line; cardinal extremities smooth, produced into slight points; plications nine to twelve per 5 millimeters at anterior margin; sexpartite cardinal process pronounced.

Types.—Holotype, F. 3764, L. 66; paratypes, F. 3554-F. 3558, F. 3559, L. 66; F. 3765-F. 3768, L. 66; University of New England Collections.

Material.—F. 3764-F. 3808, L. 66 and L. 145; University of New England Collections.

Description.—Exterior: Shells are about medium-sized for the genus and rather strongly concavo-convex, with the greatest width at the hinge line. The general outline is sub-semicircular, with a broadly rounded anterior margin and but very slightly curved sigmoidal lateral margins. Cardinal extremities are smooth, slightly turned anteroventrally, and end in slight points. There is

no distinct fold or sulcus on the brachial and pedicle valves, respectively, although there is a suggestion of these features.

The pedicle valve is moderately to rather strongly convex, having its greatest convexity at about the midlength. The interarea is very slightly concave, and slightly apsacline near the beak, becoming moderately apsacline laterally. The delthyrium is triangular, slightly wider than long, and has a strongly arched deltidium that is confined largely to about the apical one-third of the opening. The inner surface of the deltidium is covered with shelly material formed into three ridges corresponding in position to the median and first lateral grooves of the cardinal process. Cardinal spines are imperfectly known, but are relatively few, perhaps about six on each side of the beak.

The brachial valve is markedly concave just anterior to the hinge line, becoming almost flat near the anterior margin. The interarea is much shorter than that of the pedicle valve. It is essentially flat and slightly apsacline near the beak, becoming moderately apsacline laterally. A prominent sexpartite cardinal process fills the notothyrium. The narrow median pair of lobes is the largest, and separated by a thin, deep groove; these lobes become thicker and expanded as they extend internally. Each lobe of the first lateral pair is wider and shorter than each lobe of the median pair; fairly broad, rounded furrows separate the median pair of lobes from the first lateral pair. The second lateral lobes are shorter than the first lateral lobes, and separated from them by narrow, acute grooves. A strongly arched chilidium covers about the apical one-third of the cardinal process, and usually extends nearly the length of the filled notothyrium.

Radial plications cover the surface of the both valves, except on the postero-lateral slopes which are smooth. Plications number nine to twelve per 5 millimeters at the anterior margin; they frequently bifurcate, with only an occasional intercalated plication. Plications and the intervening furrows are founded in transverse profile, and furrows vary most commonly from one-third to one-half the width of the plications. The shell surface is devoid of concentric ornamention except for fine irregularly spaced growth lines.

Interior: In the pedicle valve, there is a faintly impressed flabellate muscle field which extends one-fourth to one-third the length of the valve. This muscle field partially encloses two small adductor scars, which extend from near the apex, one-half to three-fourths the length of the diductor field.

The diductor field is of two lobes, separated by a median septum, which is flanked by low ridges that are possibly pallial trunks. Subangular, strongly diverging shoulders bound the posterior margin of the diductor field. Adductor scars are elongate and teardrop-shaped, their posterior ends at about the same position as the posterior end of the diductor scars. The supposed pallial trunks appear to begin at the tip of the apex and extend forward to near the anterior margin of the valve; adductor scars are seemingly draped over them.

The median septum has a average extent of about three-fifths the length of the valve. This structure begins ventrally to, and near the apex of the delthyrium, as a slightly convex, rather high, sharp ridge. It narrows rather rapidly and almost plunges to the floor of the valve at a point slightly greater than one-half the length of the adductor scars. Then it rises gradually and widens to a broader ridge before again tapering and finally diminishing altogether.

Teeth are narrow, rounded on their anterior ends, and subparallel to the hinge line.

Oblique taleolae, pointing anteriorly and laterally, are arranged in raidal rows, corresponding in position to external furrows. These protruberances appear coarser just lateral to the diductor field, and are not seen on the cardinal points. Taleolae are produced into well-defined endospines, especially marginally.

In the brachial valve, a low median ridge extends about one-fourth the length of the valve. Flanking the median ridge are two shorter, narrower diverging ridges, approximating one-half the length of the median ridge. Posterior adductor scars are broad, rather widely diverging lobes lateral to the diverging ridges, and extending some distance in front of the tip of the median ridge.

Anterior adductor scars are at the posterior end of the posterior scars, and contained largely between the diverging ridges and the median ridge. Sockets are narrow, relatively deep, and approximately subparallel to the hinge line.

Taleolae appear coarsest and most pronounced at the middle portion of the valve, and seemingly diminish in strength marginally. Endospines are well-defined.

Measurements.—(In millimeters)

Pedicle valves

Length	Width	Length of Median Septum
ca. 11.5	ca. 18	ca. 6.5
ca. 10	ca. 16 (est.)	6
ca. 10	ca. 14	—
ca. 9.5	ca. 13	—
ca. 9	ca. 14	ca. 6
ca. 8.5	ca. 13	ca. 5.5
7	10	ca. 4

Brachial valves

Length	Width	
ca. 11	ca. 17	
ca. 10	ca. 15 (est.)	Length of median ridge, 2.5 mm.
ca. 9.5	ca. 15	
ca. 9.5	ca. 14	
ca. 9	ca. 14 (est.)	
ca. 9	ca. 14	
ca. 8	ca. 13	
7.5	13	

Remarks. — Rugosochonetes? werriensis Campbell (1957, p. 66, pl. 12, figs. 27–30) from the upper Tournaisian at Babbinboon, N. S. Wales, is similar but differs in being smaller, more transverse, and having somewhat finer radial ornament.

Internally, *Plicochonetes sexifidus*, n. sp., differs from *Chonetes gloucesterensis*, n. sp., in the more well-defined brachial adductor scars, shorter median ridge in the brachial valve, and more obliquely oriented taleolae, which are marginally produced into well-defined endospines. External differences are quite apparent.

Occurrence.—At present, this species is known only from the fossiliferous mudstone below the *"Productus" barringtonensis* bed from the upper part of the Lower Burindi group, south of Barrington, N. S. Wales; upper Tournaisian.

Suborder SPIRIFEROIDEA Allan, 1940 emend. Muir-Wood, 1955

Superfamily SPIRIFERACEA Waagan, 1883

Family SPIRIFERIDAE King, 1846

Subfamily PHRICODOTHYRINAE Caster, 1939

Genus PHRICODOTHYRIS George, 1942

Type species.—Phricodothyris lucerva George, T., 1932, p. 546–548, pl. 35, figs. 2a–d.

Diagnosis.—"Brachythrid; commissure rectimarginate, uniplicate, or parasulcate; surface ornament of concentric lamellae bearing biramous barked spines; shell structure fibrous, impunctate; apical plates and median septum of the pedicle valve may be absent or exhibit variation in strength of development; brachial valve without a concave hinge-plate and supporting median septum; a very low, narrow median septum exists between and anterior to the brachial adductor scars." (Campbell, 1955, p. 377).

Phricodothyris ranges from the Lower Carboniferous to the Permian.

PHRICODOTHYRIS CAMPBELLI, n. sp.
Pl. 111, figs. 14–20,23,25

Diagnosis.—Shells about medium-sized for genus, with well-rounded cardinal extremities; median sulcus very shallow, median fold low; concentric bands number about eight to nine per 10 millimeters on median anterior portion of shell; biramous spine bases number six to nine per 5 millimeters on median anterior portion of shell.

Types.—Holotype, F. 1339A–B; paratypes, F. 3724-F. 3726, L. 66, and F. 3733. L. 146; University of New England Collections.

Description.—Exterior: Shells are about medium-sized for the genus and the cardinal extremties are well rounded. The width of the hinge line is somewhat variable, but usually approximates one-half the width of the shell.

The pedicle valve is slightly wider than long, with a prominent convex umbo. Anteriorly, the valve is uniformly and gently convex. In transverse profile, the valve is moderately convex in the median portion and slopes rather abruptly toward the lateral margins. A very shallow sulcus, originating at the beak, is obtusely subangular

throughout most of its extent, but becomes broadly rounded at the median anterior portion of the valve. The interarea is moderately high and concave, and moderately apsacline. An open, broadly trangular delthyrium is present.

The brachial valve has a length slightly greater than two-thirds that of the width. It has a quite uniform convexity throughout its length, being just slightly more convex at the umbo. In transverse profile, the valve is broadly arched, and slopes more gradually toward the lateral margins than the pedicle valve. There is a very low rounded fold, which presumably originates at the beak. The short interarea is slightly concave and slightly anacline. It is ornamented with fine striae at right angles to the hinge line.

Both valves are ornamented with concentric bands that become crowded together around the margins. Bends number about eight to nine per 10 millimeters at the median anterior portions of the valves. The biramous spine bases are at the front margins of the concentric bands and number six to nine per 5 millimeters at the median anterior portions of the valves.

Interior: In the pedicle valve, a thin sharp median septum extends from more than one-half to about three-fifths the length of the valve. Narrow dental lamellae, diverging at angles of about 22 to 38°, extend approximately one-half the length of the median septum. The diductor field is poorly defined and poorly impressed. Diductor scars begin anterior to the apex; their anterior margins continue from the tips of the dental lamellae toward the tip of the median septum where they meet at an acute angle. Surfaces of the scars are covered with low, rounded longitudinal ridges. Radiating striae, with their focus near the posterior end of the muscle field, may cut across the ridges. Adductor scars are narrow, elongate impressions flanking the median septum and extending to the anterior tip of it. Adductor scars do not extend the entire length of the diductor field.

Teeth are narrow and acute on their inner edges. The surface of the valve is covered with numerous, small and wavy longitudinal ridges, which are coarser and more wrinkled around the muscle field. These ridges diminish in strength marginally before disappearing altogether at the extreme margins.

In the brachial interior, a low narrow median ridge extends about three-fifths the length of the valve. Adductor scars are very shallowly impressed and poorly defined, so they can not be differentiated with certainty. They appear as relatively smooth areas on the otherwise longtitudinally ridged surface of the valve. Ridges are similar to those on the pedicle valve, and again are coarser around the muscle field. Sockets are approximately subparallel to the hinge line, shallow and rather flat. Crural plates are slightly concave inward. The cardinal process consists of numerous thin platelets.

Measurements.—(in millimeters)

Pedicle valves

Length	Width	Width of Hinge Line	Length of Median Septum	Angle of Divergence of Dental Lamellae
ca. 34 (est.)	35	—	ca. 17.5	—
31	ca. 34	ca. 20	16	22°
27.5	34	16	15.5	26°
ca. 27	ca. 32.5	15	17	29°
ca. 26.5 (est.)	32	14	15	38°
22	25	13	12	32°

Brachial valves

Length	Width	Width of Hinge Line	Length of Median Ridge
ca. 25	31.5	20	15
23	ca. 36 (est.)	ca. 18 (est.)	15
22	31	16	13
20.5	ca. 28 (est.)	ca. 11 (est.)	—
19	28	ca. 12 (est.)	—
18.5	28.5	—	—

Remarks.—*P. triseptata* Campbell from the upper Tournaisian at Babbinboon, N. S. Wales (Campbell, 1955, pp. 379–380, pl. 18, figs. 10–15) is rather similar, but there are notable differences. An examination of the holotype and figured specimens revealed this species to be more transverse, with a less well-defined median sulcus, and a wider hinge line, resulting in somewhat less rounded cardinal extremties. Also, the median septum in the pedicle valve is shorter, and the median ridge is the brachial valve is shorter.

Occurrence.—This species is, at present known only from the fossiliferous mudstone below the "*Productus*" *barringtonensis* bed from the upper part of the Lower Burindi group, south of Barrington, N. S. Wales; upper Tournaisian.

PHRICODOTHYRIS sp.
Pl. 111, figs. 21,22,24,26

Diagnosis.—Shells large for genus, transverse; rather shallow median sulcus on pedicle valve; concentric bands number about 14 to 18 per 10 millimeters, biramous spine bases number about 20 to 25 per 5 millimeters on median anterior portion of pedicle valve.

Material.—F. 3743–3763; L. 66, L. 146 and L. 147, University of New England Collections.

Description.—*Exterior:* The shell is large for the genus, and has rounded cardinal extremities. The hinge line approximates three-fifths the width of the shell.

The pedicle valve is slightly wider than long, with the greatest width at about the midlength. The umbo is prominent, and the beak is rather strongly incurved at the tip. Anteriorly, the valve profile is rather gently arched. In transverse profile, the valve slopes gradually laterally, and forms a very slight concavity before reaching the lateral margins. A broadly rounded, rather shallow sulcus extends from the beak to the anterior margin, where the valve is produced into a short, well-defined rounded lobe. The interarea is concave, moderately high, and moderately apsacline. The delthyrium is open, and broadly triangular.

Ornamentation is dense and pronounced. Concentric bands number about nine to twelve per 10 millimeters of the median posterior portion, and about 14 to 18 per 10 millimeters on the median anterior portion of the valve. Bands become crowded together marginally, spine bases are numerous, numbering about 20 to 25 per 5 millimeters on the median anterior portion of the valve.

At present, the brachial valve is unknown in this species.

Interior: A sharp, narrow median septum extends about three-fifths the length of the pedicle valve. Flanking the septum are sharp, thin dental lamellae which extend from about one-fourth to one-third the length of the valve, and diverge at angles of about 51 to 60°. Diductor scars are moderately well impressed, and contained between the diverging dental lamellae and the median septum. Diductor scars begin forward of the apex, and from the ends of the dental lamellae, their margins converge anteriorly toward the median septum, where they meet at a large acute angle. Surfaces of the diductor scars are marked with low rounded longitudinal ridges, which are slightly broader continuations of the narrow ridges covering almost the entire surface of the valve. The muscle field area is somewhat smoother than the surrounding portions of the valve. Curved radiating ridges may also be present on the diductor scars, the focus of radiation being at the posterior portion of the muscle field. Adductor scars appear as narrow elongate impressions on either side, and adjacent to, the median septum.

The surface of the valve is covered with numerous thin radiating ridges which gradually diminish marginally, and disappear on the extreme margins. These ridges are coarser and become sinuous lateral to the muscle field; they increase by bifurcation and intercalation. Teeth are narrow and acute on their inner edges.

Measurements.—(in millimeters see next page).

Remarks.—This species can be easily distinguished from *P. campbelli*, n. sp., by its generally larger size, larger divergent angles of the dental lamellae, and the more numerous concentric bands and spine bases.

P. uniplicata Campbell from the upper

Pedicle valves

Length	Width	Width of Hinge Line	Length of Median Septum	Muscle Field		Angle of Divergence of Dental Lamellae
				Length	Width	
ca. 35	ca. 43 (est.)	ca. 27 (est.)	20	17.5	11.5	51°
ca. 36	43	ca. 24	22	18.5	13	44°
ca. 36 (est.)	ca. 45.5	26	21	17	12	60°
ca. 35 (est.)	ca. 48 (est.)	ca. 27.5	ca. 22	17	11.5	53°

Tournaisian at Babbinboon, N. S. Wales (Campbell, 1955, p. 377–379, pl. 18, figs. 1–9) is a related species, but has certain differences. The holotype and figured specimens were examined. This species is slightly more transverse, has less rounded cardinal extremities, and a deeper and better defined median sulcus. Also, the greatest width of the shell is slightly more posterior than in the present species, and the diductor scars are not so well defined.

The present form was not assigned to any definite species for, at present, only the pedicle valve is known. After discovery of the brachial valve, a later worker may complete the description and establish the specific designation. It is important to have the most information possible when engaged in taxonomy, especially if the forms concerned are new, as is probably the present form.

Occurrence.—This species is at present known only from the fossiliferous mudstone below the "*Productus*" *barringtonensis* bed from the upper part of the Lower Burindi group, south of Barrington, N. S. Wales; upper Tournaisian.

Subfamily SPIRIFERINAE King, 1846
Genus SPIRIFER Sowerby, 1816

Type species.—(by suspension of the Rules by the International commission on Zoological Nomenclature, Opinion 100) *Conchyliolithus Anomites striatus* Martin, W., 1793, "Figures and Descriptions of Petrifactions Collected in Derbyshire, pl. 23, figs. 1,2 and Martin, W., 1809, "Petrificata Derbiensia", pl. 23, figs. 1,2.

Partial diagnosis.—Shell subequally biconvex, usually wider than long, with the greatest width at the hinge line; median fold and sulcus present; surface covered with numerous costae, including the fold and sulcus; costae are simple, or split occasionally or frequently, but are never strongly fasciculate.

Remarks.—It is difficult to ascertain just what the essential characters of *Spirifer s.s.* are. The holotype is apparently lost. Examination of the type description and figures is most disconcerting, as little information can be gained from them. Some information on the type species has been given by Harrington & Leanza (1952), who say *Spirifer striatus* (Martin) has relatively short divergent dental lamellae and no delthyrial plate. Even after this is considered, however, a great deal of information regarding the genus is yet lacking. Therefore, the present species is not with certainty assigned to the genus *Spirifer*.

SPIRIFER LIRELLUS, n.sp.
Pl. 112, figs. 1–7,11; text-figs. 5,6

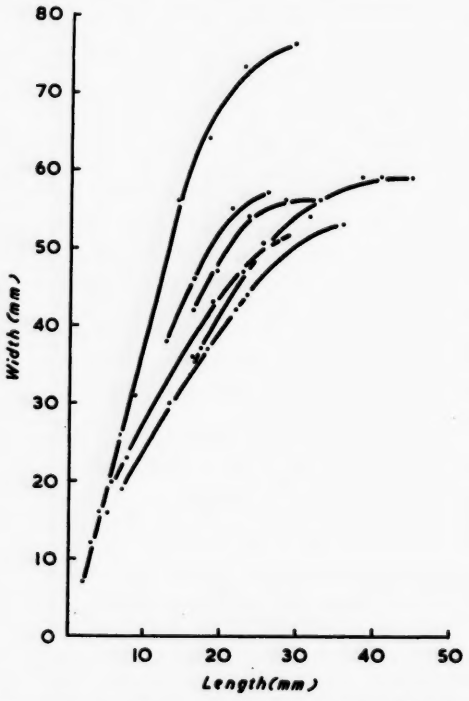
Diagnosis.—Shells usually wider than long; cardinal extremities strongly mucronate in early growth stages, but slightly pointed in later stages; length/width ratio increases with age (see text-fig. 5); multicostate, costae number about 75 to 90; surface covered by fine radial lirae, about 10 to 12 per 1 mm.

Types.—Holotype, F. 3611A–B, L. 66; paratypes, F. 3621A–B to F. 3619, University of New England Collections.

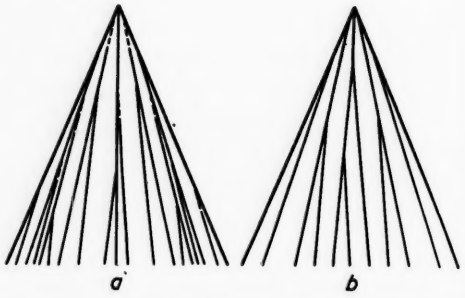
Material.—F. 3611—F. 3676, University of New England Collections.

Description.—Exterior: Shells are large, and usually wider than long, the greatest width at the hinge line, or between the hinge line and the midlength. Cardinal extremities are short and pointed, but not sharp; they are slightly turned ventrally. In early growth stages, cardinal extremities are extremely mucronate, produced into elongated points. With increasing growth,

these extremities become shorter and less pointed. It should be mentioned that in very early growth stages, (*i.e.*, a very limited area confined to the beak in adult specimens,) the cardinal extremities are rounded and curve inward, but quite rapidly form the mucronate extremities. Three of the largest and most complete pedicle valves had the following measurements (in millimeters): Length, ca. 56, ca. 53, and ca. 64 (est.); width, ca. 70 ca. 62(est.), and ca. 62. The pedicle valve is rather strongly convex, its greatest convexity within about the posterior one-half of the length. Anterior to the midlength, the valve is almost flat to very gently convex. In transverse profile, the valve slopes rather rapidly laterally before becoming slightly concave on the extreme lateral slopes. The shallow sulcus, originating at the tip of the beak, is obtusely subangular in early growth stages, becoming broadly rounded in later stages. At the anterior margin, the sulcus



TEXT-FIG. 5—Scatter diagram of length/width the brachial valves of six specimens of *Spirifer lirellus*, n. sp., from near Gloucester, New South Wales; individual ontogenies are shown.



TEXT-FIG. 6—Diagrammatic representation of the sinal costae in *Spirifer lirellus*, n. sp. (5a) from near Gloucester, New South Wales, compared with that of *Spirifer tornacensis* de Koninck (5b) from Belgium.

continues on to a narrowly rounded lingual extension which occasionally becomes quite produced. The interarea is high and moderately apsacline, being flat or slightly concave throughout most of its extension. Near the beak it is moderately to strongly concave.

The delthyrium is large, and higher than wide. It has variable amounts of callus, which is deposited in the apex and along the inner surfaces of the dental lamellae. Narrow ridges bound the delthyrium and continue on the inner edges of the teeth. Narrower grooves, in turn, laterally border the ridges.

Numerous hinge denticles are present on the anterior margin of the palintrope as discussed by Glennister (1955, p. 48) in *Spirifer fluctuosus* Glennister from the Carboniferous of Western Australia. These denticles, which are less pronounced and originate near the margin of the delthyrium, articulate with shallow denticle pits in the brachial valve. Shallow irregularly spaced denticle grooves, on the surface of the interarea and at approximate right angles to the hinge line, trace the ontogeny of the denticles. Bifurcation of denticle grooves occasionally occurs.

This sections cut normal to the surface of the interarea, reveal that hinge denticles are more or less separate units. Calcite fibers can be seen to curve around the denticles. If thin layers of shell are broken from the surface of the interarea, pronounced grooves are seen, for the denticle units sepa-

rate readily from the curved calcite fibers. Calcite of the denticles is non-fibrous, or at any rate, oriented much differently from other calcite fibers of the palintrope. On weathered specimens, the denticles weather more readily, leaving abnormally pronounced denticle grooves.

The brachial valve is much less convex than the pedicle valve and rather uniformly convex throughout its length although slightly more convex at the umbo. Transversely, the profile slopes gradually on to the slightly concave extreme lateral slopes. The fold is moderately high and rounded but has a definite apex, and approximately subangular in early growth stages. The interarea is much smaller than that of the pedicle valve and moderately anacline. It is similar in lateral profile to that of the pedicle valve, *i.e.*, almost flat or but slightly concave throughout most of its extension, but may become rather strongly concave near the beak. Shallow denticle pits, for the reception of the hinge denticles, are present along the anterior margin of the palintrope.

Both valves are covered with low, rounded costae, which number about 75 to 90 at the commissure. Costae number approximately 19 in the sulcus and on the fold. Costae bifurcate, occasionally on the lateral slopes, and frequently in the area of the fold and sulcus. Bifurcation is usually not equal, but more commonly one branch is subordinate. There are usually three costae in the median portion of the sulcus; they are extremely variable in their positions of differentiation, which may occur at the posterior or anterior portions of the valve, or most irregularly and at random. On the fold, subordinate branches of costae are usually outermost, while in the sulcus, they are usually innermost. Costae are separated by narrow, subangular to subrounded furrows, about one-third to one-half the width of the costae.

Also covering the surface of the shell are extremely fine radial lirae, numbering about 10 to 12 within the space of 1 millimeter. Lirae are separated by rounded furrows, which may be less, equal to, or greater in width than the lirae. Occasional irregularly spaced growth markings cross the fine radial lirae, but do not give a grid-like appearance as is found in some Spirifers, e.g., *Spirifer striatoparadoxus* Toula (Dunbar, 1955, p. 133).

Interior: In the pedicle valve is a commonly suboval muscle field, produced anteriorly, and extending about two-fifths the length of the valve. This muscle field varies greatly in depth of impression, but is always impressed more posteriorly. The outer large diductor scars are radially crenulated, the focus of radiation at about midlength of the muscle field. Commonly, low rounded longitudinal ridges and furrows also ornament the diductor scars. Adductor scars are narrow and elongate, occupying a subcentral position within the diductor field, or slightly posterior. Separating the adductor scars is a narrow median ridge, extending to near their anterior tips. From here it may continue as a lower ridge, become flattened, or be replaced by a groove to the tip of the diductor field.

Dental lamellae, diverging about 40 to 55°, are relatively short, extending to about the posterior one-third of the muscle field. The apical portion of the delthyrial cavity is variously filled with adventitious shell material, as are the umbonal cavities lateral to the dental lamellae. The narrow, pointed teeth have their sharp, acute lower edges turned rather strongly inward.

Numerous pitlike genital markings are limited to the posterior portion of the valve surrounding the muscle field, continuing on the inner surface of the interarea. Markings are most pronounced just laterally to the dental lamellae.

In the brachial valve, a low sharp and narrow median ridge extends about one-half the length of the valve. This ridge is flanked by two narrow, short, narrowly diverging ridges, extending about one-fourth the length of the median ridge. Diverging ridges are occasionally poorly defined, especially on younger individuals. Adductor scars are rather broadly elongate imprints, separated by the median ridge, and characteristically have a roughened surface. They extend from a point just anterior, or some distance, from the ends of the diverging ridges to about the tip of the median ridge. These scars are almost wholly confined to the trough (corresponding to the external fold). Posterior adductor scars are much narrower and more

elongate imprints lateral to the diverging ridges. In front of the ends of the diverging ridges they usually curve somewhat inward and continue forward some distance along the flanks of the anterior scars.

Genital markings are restricted to a very small area in the posterior portion of the valve, mainly just lateral to the diverging ridges. Markings do not become as pronounced as those on the pedicle valve.

Sockets are narrow and widely diverging, supported by rather straight socket plates. Crural plates bounding the sockets on their innermost surfaces appear quite flat on their inner surfaces. The cardinal process is composed of numerous platelike ridges, about 23 to 38, and wider than the spaces betweeen them.

Remarks.—Specimens are commonly distorted. Pedicle valves may be arbruptly bent at about the posterior one-third of the length. If the anterior two-thirds of the shell is missing, one gets the incorrect impression of a species with a very wide hinge line and much produced cardinal extremities. Brachial valves are also commonly crushed, making it difficult to determine essential characters.

This species appears rather closely comparable with *Spirifer logani* Hall from the Keokuk limestone (Osagean) of the United States. However, *S. logani* is somewhat larger, broader, and has a more broadly triangular delthyrium. Also, the pedicle muscle field tapers more posteriorly, instead of anteriorly as in the present species.

Casts of the syntypes of *S. tornacensis* de Konick were examined. This species has similarities, but differs in being somewhat shorter, having more produced cardinal extremities, fewer costae in the sulcus, (see text-fig. 5) and a microscopic gridlike ornament of both radial and concentric lirae. *S. suavis* de Konick is also possibly quite similar. According to Vaughan (1915, p. 42), both species occur at the top of the Petit Granit in Belgium, or what is equivalent to the C_1 zone of the South-Western Province of England (Correlation chart facing p. 32).

It is difficult to make accurate comparisons with the type species, *S. striatus* (Martin). However, a plaster cast of a young specimen (topotype?) from Treak Cliff, near Castleton, Derbyshire, England was examined. It shows growth lines which are rounded and curve inward at the posterior margin, opposite to that of *S. lirellus*, n. sp., in which the growth lines extend outward toward the cardinal extremities.

The specific name is derived from the Latin *lirella*, diminutive of *lira* 'a ridge', referring to the numerous fine radial lirae covering the surface of the shell.

Occurrence.—To date, this species is known only from the fossiliferous mudstone below the "*Productus*" *barringtonensis* bed from the upper part of the Lower Burindi group south of Barrington, N. S. Wales; upper Tournaisian.

Genus TYLOTHYRIS North, 1920

Type species.—*Cyrtia laminosa* McCoy, 1844, Carb. Foss. Ireland, p. 137, pl. 21, fig. 4.

Diagnosis.—Shells spiriferoid, about twice as wide as long, with greatest width along hinge lines; sulcus wide and subangular, mesial fold distinct, subangular plications on lateral slopes; surface of valves covered by regularly spaced growth lamellae; shell fibrous and impunctate; pedicle valve with dental lamellae and well developed median septum; brachial valve with low median ridge (abstracted from North, 1920, p. 195-196).

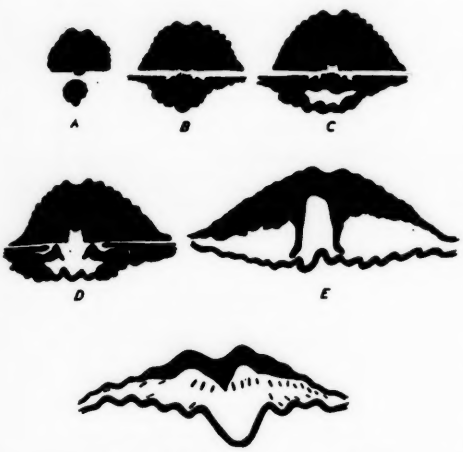
Remarks.—In North America, this genus ranges from the upper Devonian to the Mississippian. North gives the range of *Tylothyris* as the Carboniferous Limestone, from *Cleistopora* zone to the upper *Dibunophyllum* zone; that is, throughout the Avonian or Dinantian.

This is the first reported occurrence of this genus in New South Wales.

TYLOTHYRIS PLANIMEDIA, n. sp.
Pl. 112, figs. 8–10,12; pl. 113, figs. 1–5; text-fig. 7

Diagnosis.—Shells large for genus, cardinal extremities mucronate; narrow, median portion of sulcus flat; nine to fourteen plications on each lateral slope; surface covered with gridlike micro-ornament of fine radial and concentric lirae.

Types.—Holotype, F. 3391A–B; paratypes, F. 3392A–C, F. 3394, F. 3395, L. 146,



TEXT-FIG. 7—Serial sections through the umbonal region of *Tylothyris planimedia*, n. sp. (×I), from near Gloucester, New South Wales. Fig. 7A, at 1 mm. from the tip of the umbo; fig. 7B, at 1.5 mm.; fig. 7C, at 2 mm.; fig. 7D, at 2.5 mm.; fig. 7E, at 4.5 mm.; and fig. 7F, at about 11 mm. The brachial valve, which is lowermost in all sections, is somewhat distorted.

University of New England Collections.

Material.—F. 3391-F. 3421, University of New England Collections; collecting localities L. 66, L. 145, L. 146, and L. 148.

Description.—Exterior: The pedicle valve is about three-fifths as long as wide, with the greatest width at the mucronate cardinal extremities. The shell is more greatly convex at the umbo, becoming less so anteriorly. Latero-posterior margins are narrowly ridged, the ridges increasing in prominence laterally. A prominent subangular sulcus extends from the tip of the beak to the anterior margin, where it continues as a narrow lingual extension. The narrow medial portion of the sulcus is flat, the flat area becoming somewhat less sharply defined anteriorly. At the anterior margin, the sulcus is about equal in width to four adjacent costae and their intervening furrows.

The interarea is concave, moderately high and apsacline. The delthyrium is triangular, wider than high and virtually open, except for a short teardrop-shaped apical filling which swells away from the apex. Some callus infilling is present on the inner surfaces of the delthyrium. Bordering the delthyrium are narrow ridges which continue brachially on to the teeth. Narrower grooves border laterally the narrow ridges.

The brachial valve is about twice as wide as long, and less convex than the pedicle valve. It does not have a more convex umbo, but is quite uniformly convex from beak to anterior margin. Ridges are present on the latero-posterior margins but not as well developed as on the opposite valve. The fold is subangular, but has a well rounded summit. Width of the fold is about equal to the width of four adjacent costae and their intervening furrows. The interarea is low, slightly concave and strongly anacline. No medial opening is present along the interarea, its position being completely occupied by the broad cardinal process.

Plications are rather narrowly rounded, with subangular intervening furrows; on either side of the fold or sulcus they number nine to fourteen (counting at the anterior margin). On the extreme lateral slopes, plications are rather faint and somewhat wrinkled; bifurcation may occasionally occur. The regular concentric lamellae have a density of about 12 to 15 per 5 millimeters near the anterior margin. A micro-ornament of very fine radial and concentric lirae produces a gridlike effect when viewed under high magnification. The fine radial lirae, with furrows of about equal width, number about 22 to 28 per 1 millimeter. Concentric lirae are of similar dimensions.

Interior: The pedicle muscle field is moderately impressed and approximately suboval; its posterior margin is rather blunt. The anterior margin of the field extends about two-fifths the length of the valve. Diductor scars are more deeply impressed medially, the intensity of impression decreasing laterally. Low ridges on the scars radiate in all directions from a point at about midlength of each scar. Separating the diductor field is a sharp, high and narrow median septum, which reaches its maximum height just before terminating at, or just short of, the end of the diductor field. Adductor scars are narrow, elongate impressions flanking the median septum. They begin at the margin of the relatively short apical callosity and may or may not extend to the anterior margin of the septum. Pos-

teriorly, adductor scars are flanked by narrow ridges on their lateral margins.

Teeth are narrow and sharp, their edges pointing inward at a high angle. Dental lamellae continue from the edges of the teeth to the floor of the valve, terminating near midlength of the diductor field. Dental lamellae diverge at angles of about 35 to 54°.

Ovarian markings are restricted mainly to an area on either side of the diductor field, with some markings continuing around the anterior margin of the field. These pitlike depressions are deepest just lateral to the best defined portions of the dental lamellae, and on the inner surfaces of the interarea just lateral to the teeth. Numerous, poorly defined, narrow rounded ridges arising from the margins of the ovarian area are possibly pallial markings. Gerontic individuals show a pedicle interior which has a thicker apical callosity, much broader diductor field, and a coarser ovarian area.

In the brachial valve, the lenticular posterior adductor scars are narrow and elongate, tapering gradually to a narrow point anteriorly. These scars are on the ridges (corresponding to external furrows) bounding the large median trough (corresponding to the external median fold); they extend about two-fifths the length of the valve, beginning just anterior to the cardinal process. Exact shape and extent of anterior scars is unknown, but the scars are located along the flanks of the median trough and are broader than the posterior scars. The very low, sharp and narrow median ridge extends approximately one-half the length of the valve.

Sockets are narrow, well-defined and widely divergent. Sharp, narrow crural plates separate the sockets from the broad cardinal process. The cardinal process consists of about 20 sharp, thin sinuous platelets. A very short apical callosity is present.

In the pedicle valve, the shell is much thicker in the umbo than in the brachial valve. This is brought out strikingly by serial sections as can be seen in text-figure 7. Each spire of the spiralium has about 16 volutions; the jugum was not observed.

Measurements.—(in millimeters)

Pedicle Valves

Length	Width	Angle of Divergence of Dental Lamellae	Muscle Field		Length of Median Septum
			Length	Width	
ca. 28	ca. 46.5	45°	10	8	14
28	ca. 40	ca. 35°	9	7.5	11
ca. 26 (est.)	ca. 42 (est.)	48°	8.5	8.0	—
ca. 25	ca. 42 (est.)	40°	ca. 7	6.5	13.5
ca. 24	ca. 41 (est.)	50°	7.5	7.5	12
ca. 23	ca. 41		Mold of exterior		
ca. 23 (est.)	ca. 40 (est.)	40°	8	5.5	ca. 12
ca. 23	ca. 38 (est.)		Mold of exterior		
ca. 22	36.5	45°	5.5	5	9
ca. 20	ca. 34 (est.)	40°	ca. 7.5	ca. 6	11.5
ca. 18	ca. 30	ca. 30°	4	4	7
ca. 18	ca. 28	38°	5	5.5	7
ca. 17	ca. 27	38°	6	5	ca. 7

Brachial Valves

Length	Width	Length of Median Ridge	Height of fold
ca. 24	ca. 50	—	ca. 7
ca. 23	ca. 47	—	ca. 6
ca. 20	ca. 40	—	ca. 5.5
20	ca. 40	—	ca. 6
19	ca. 39 (est.)	—	ca. 5
13	ca. 27	6	—

Remarks.—The writer is not aware of any species of *Tylothyris* closely comparable to the present species. It differs from the type species in being larger, having mucronate

cardinal extremities, more numerous plications, and a flat median portion in the sulcus.

The specific name, *planimedia*, is derived from the Latin *planus* 'flat' and *medius* 'middle,' referring to the flat median portion of the sulcus.

Occurrence.—This species is at present known only from the fossiliferous mudstone below the "*Productus*" *barringtonensis* bed from the upper part of the Lower Burindi group, south of Barrington, N. S. Wales; upper Tournaisian.

Superfamily PUNCTOSPIRACEA Cooper, 1944

Family SPIRIFERINIDAE Davidson, 1884

Genus PUNCTOSPIRIFER North, 1920

Types species.—*Punctospirifer scarbricostus* North, 1920, p. 213, text-figs. 1p,4h, and 5g, pl. 13, fig. 6.

Diagnosis.—Spiriferoid shells having greatest width at or near hinge line, cardinal extremities slightly rounded or subangular; ornamented by regularly spaced growth lamellae on which are gradually thickening spine bases giving rise to spines; broad, rounded fold and wide shallow sulcus, numerous rounded costae on lateral slopes. Pedicle interior with strong dental lamellae and well developed median septum; brachial interior with low median ridge; jugum V-shaped, possibly directed anteriorly. Shell strongly punctate.

Remarks.—North (1920) fails to mention spines in members of this genus, although spines are apparently present. Dr. H. M. Muir-Wood (British Museum) indicates (written communication) that the holotype (*P. scarbricosta mut. ashfellensis* North, Garwood Collection, Geol., Survey Museum, London, G. S. no. 64285) possesses spine bases. Also, a photograph of the median sulcus of *P. scarbricosta mut. redesdalensis* North (British Museum, BB10099) clearly shows anteriorly thickened spine bases on the growth lamellae.

Stehli (1954, p. 345), indicates North is probably mistaken about the way the jugum is directed. According to Stehli, various Paleozoic genera of the Spiriferinidae examined by him showed the jugum to be anteriorly directed, in exact opposition to North's observations.

This genus differs from *Spiriferellina* Fredericks 1919 (type species *Terebratulites cristata* Schlotheim, upper Permian) in having more numerous and less angular costae, and a broader median fold and shallower sulcus. Also, *Spiriferellina* has less prominent concentric growth lamellae which are irregularly spaced.

Spiriferina d'Orbigny 1850 (types species, *Terebratulites rostrata* Schlotheim, lower Jurassic) has little resemblance to *Punctospirifer* but is mentioned because of its confusion with *Spiriferellina*. Fredericks (1927, pl. 1, figs. 8 and 16) figured sections through the umbo of *Spiriferellina cristata* (Schlotheim) and *Spiriferina rostrata* (Schlotheim). The former has a true median septum, whereas the latter has a pseudoseptum formed by the fusion of outgrowths of the delthyrial plate. Paeckelmann (1931, p. 50) supported the observations of Fredericks in the differences of the septum in Paleozoic and Mesozoic Spiriferinas.

Dunbar (1955) is quite probably mistaken in his reference of a Permian species from Greenland to *Punctospirifer*. This species, called *P. cristata* (Schlotheim), appears to be a rather typical representative of *Spiriferellina*.

Muir-Wood (1948) discusses *Punctospirifer*, giving as its range Devono-Carboniferous (transitional Malevka Beds of the Moscow Basin) to the Permian (of North America). In Great Britain, this genus has only been reported from the Viséan; in the European Tournaisian, *Punctospirifer* is usually replaced by *Tylothyris*.

PUNCTOSPIRIFER AMBLYS, n. sp.

Pl. 113, figs. 6–16

Diagnosis.—Shells of medium size for genus, greatest width anterior to hinge line at about posterior one-third of length; cardinal extremities blunt, well rounded in early growth stages, becoming almost subrectangular in adult stage; each lateral slope with seven to nine plications; growth lamellae number nine to twelve per 5 mm. near anterior margin; lamellae covered with numerous minute spines.

Types.—Holotype, F. 3552, L. 66; paratypes, F. 3533A–B, L. 145, F. 3538A–B and

F. 3550, L. 66; University of New England Collections.

Material.—F. 3533-F. 3552 and F. 3556-F. 3561, L. 66, L. 145, L. 146 and L. 147; University of New England Collections.

Description.—Exterior: Shells have their greatest width anterior to the hinge line, near the posterior one-third of the shell length. Cardinal extremities are characteristically blunt; in early growth states they are well rounded, curving inward toward the beak. In the adult stage, the extremities become almost subrectangular, with but a very slight curve and may form a low obtuse angle with the posterior margin.

The pedicle valve has a length just under three-fourths that of the width. It is moderately convex in lateral profile, having a greater convexity at the umbo. The interarea is concave and moderately high, about one-fifth the width of the hinge line, and moderately obtuse. The delthyrium is narrowly triangular and open. The rounded sulcus is relatively shallow, having a height about one-fourth the width. It has a width about equal to three adjacent costae and their intervening furrows.

The brachial valve is rather uniformly convex, but with a lesser convexity than the opposite valve. The fold is moderately high, and almost subangular in profile but well rounded at the summit. Its width is about equal to three adjacent costae and their intervening furrows. The interarea is much shorter than that of the pedicle valve and but slightly concave. It is very strongly obtuse, almost forming a straight angle with the lateral commissure.

Both valves have, on each lateral slope, seven to nine rounded costae separated by rounded furrows. Furrows are about one-half the width of costae near the sulcus and fold, but become about equal in width to costae on the extreme lateral slopes. The regular growth lamellae are fairly numerous, numbering about nine to fifteen per 5 mm. near the anterior margin.

Numerous hollow minute spines are inclined at a moderately acute angle to the surface of the shell. Minute spines begin well back on the growth lamellae as gradually thickening spine bases. Spine bases number nine to sixteen per 1 millimeter over the surface of the shell.

Interior: In the pedicle valve, a high, sharp median euseptum extends about seven-sixteenths the length of the shell, bisecting the adductor field. Rather short dental lamellae, diverging at angles of about 22 to 30°, extend about two-fifths the length of the septum; these lamellae meet the floor of the valve obliquely. The diductor muscle field is elongate and partially enclosed by the diverging lamellae. The margin of the diductor field extends some distance from the ends of the dental lamellae and then converges anteriorly, meeting at the tip of the euseptum at an acute angle. The two costae bordering the sulcus pass through the diductor field, but most of the muscle field is within the sulcus. Some specimens suggest, and others quite clearly show, what seem to be puncta in the area of the diductor field. This is quite irregular, for one can not imagine caeca passing through the muscle field. Perhaps this seeming paradox can be explained by punctate shell material, underlying the muscle field, being covered only by a relatively thin veneer of material for muscle attachment. Impressions of puncta would then be observed showing through the muscle field area. Adductor scars are not discernible but probably are narrow elongate structures flanking the euseptum.

The narrow teeth extend from the beak, where they are connected with the dental lamellae, on the inner surface of the interarea bounding the delthyrium. They are acute on their lower edges and just protrude as blunt points past the margin of the hinge. No apparent apical callosity is present.

In the brachial valve, a very low median ridge extends about three-fourths the length of the valve. On either side of this ridge are two conspicuous ridges on ridges (corresponding in position to external furrows) bordering the median trough (fold of the exterior). These conspicuous ridges originate near the cardinal process, and become very sharp anteriorly, before curving into the trough and terminating as broad flat flanges at a length about seven-sixteenths that of the length of the valve. Posterior adductor scars are very narrow anteriorly tapering imprints, which lie adjacent to the crural plates, and on the low rounded ridges bordering the trough. These scars are bounded on their inner edges by sharp ridges, portions

on the main conspicuous ridges. Anterior adductor scards are broad imprints along the flanks of the trough and separated by the median ridge. The anterior adductor field begins behind the front end of the posterior scars, and is bounded anteriorly by the inward curving flangelike extensions of the conspicuous brachial ridges.

Sockets are narrow and widely diverging, supported by flat, straight socket plates. Crural plates are conspicuous spoonlike structures with their inner surfaces concave, quite sharply so in that portion closely adjacent to the brachial ridges. The cardinal process is rather broad, consisting of possibly 14 narrow platelets separated by narrower furrows.

Both valves are strongly punctate, about eight to eleven puncta within the space of one millimeter; puncta have a density of approximately 64 to 121 per square millimeter. Diameters of puncta range from .025 to .075 millimeter.

Measurements.—(in millimeters)

Brachial Valve

Length	Width	Length of brachial ridges
ca. 12.5	ca. 22	ca. 5.5

Pedicle Valves

Length	Width	Length of Euseptum	Angle of Divergence of Dental lamellae
ca. 17	ca. 23	ca. 7.5	ca. 30°
ca. 15	—	ca. 7	ca. 28°
ca. 11.5	ca. 16	5	ca. 22°

Remarks.—Since there is also another lamellose spiriferoid in this fauna (*Tylothyris planimedia*, n. sp.), some confusion may at first be found, especially if broken fragments are dealt with. However, there are easily recognized differences. Even in very young shells, *T. planimedia* has acute cardinal extremities. Further, this species has a radial and concentric micro-ornament, is without spine bases, and the sulcus is flat in the median portion; also, costae are more numerous. This form is also impuctate, as is characteristic of the genus *Tylothyris*.

Punctospirifer subellipticus (McChensey) from the New Providence shale (Kinderhookian and Osagean) of the U. S. is remarkably similar; however, externally it has more rounded cardinal extremities and a lower fold. In the brachial valve, it has supposedly longer brachial ridges bordering the muscle field, extending to the anterior margin (Weller, 1914, p. 295).

P. pahangensis Muir-Wood from the Viséan of Malaya is similar, but is widest at the hinge line and has a higher pedicle interarea.

The specific name *amblys* is taken from the Greek word *'αμβλύs* 'blunt', referring to the blunt cardinal extremities.

Occurrence.—This species is at present known only from the fossiliferous mudstone below the *"Productus" barringtonensis* bed from the upper part of the Lower Burindi group, south of Barrington, N. S. Wales; upper Tournaisian.

Phylum MOLLUSCA Linnaeus, 1758
Class CEPHALOPODA Cuvier, 1798
Suborder AMMONITOIDEA Haan, 1825
Family GONIATITIDAE de Hann, 1825, emend. Delépine, 1952
Genus BEYRICHOCERAS Foord, 1903

Type species.—*Goniatites obtusus* Phillips, John, 1826, Illustrations of the geology of Yorkshire. . . , part 2, The Mountain limestone district.

Diagnosis.—External lobe less deep and broader than in *Muensteroceras*; margins of ventral lobe not straight, but flexed and diverging toward external margin; median saddle higher in adult; surface ornament of transverse striae and flexuous, falciform costae (after Delépine, 1940a, p. 62).

Remarks.—Miller (1947, p. 19–20) discusses the validity of the name *Beryrichoceras* because of doubt as to what should be the type species. If the type species, as designated by Bisat (1924), *Goniatites obtusus* Phillips, is used, then *Beyrichoceras* is acceptable. However, it seems that *Goniatites obtusus* Phillips is a junior synonym of *Ellipsolites ovatus* Sowerby, the type species of *Nautellipsites* Parkinson. Miller adds that he examined Sowerby's illustration and description and that both were too inadequate to make any acceptable decision. Therefore, until the type specimens are restudied, he prefers to retain the name *Beyrichoceras* and the type species as designated by Bisat. This course of action is adopted herein.

There appears to be no little confusion

regarding the geologic range of this genus. According to Miller (1947, p. 21), *Beyrichoceras* in Europe is characteristic of the middle Viséan, zone B of Bisat (1924) and zone IIIα, of Schmidt (1925). However, Delépine (1940a, p. 63–73) describes nine species of *Beyrichoceras* from Belgium and reports they are found in the D_1 and D_2 zones of the upper Viséan. Then Gignoux (1955, p. 167) says, ". . . the lower Viséan is characterized (especially in England) by the flowering of *Beyrichoceras*. . . ."

In North America, Weller, *et al.* (1948) place the zone of *Beyrichoceras* in the Osagean series (upper Tournaisian), although the upper boundary of the zone is queried. They add (p. 108):

> . . . In Europe this genus is characteristic of beds equivalent age to those which carry the lithostrotionoid coral faunas suggestive of the Meramecian. The American Meramecian is almost certainly of Viséan age, and the crinoids and brachiopods of the Osagean appear to ally this series with the Tournaisian. Consequently *Beyrichoceras* probably appeared somewhat earlier in American then in Europe.

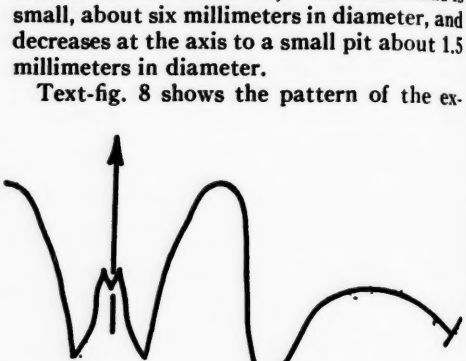
Muensteroceras Hyatt differs from *Beyrichoceras* in having the sides of the ventral lobe subparallel and ornament of transverse striae and sometimes slightly developed sigmoidal costae. *Beyrichoceratoides* Biast has an external suture similar to *Muensteroceras*, but ornament like that in *Beyrichoceras*, with transverse striae and flexuous, falciform costae.

BEYRICHOCERAS sp.
Pl. 113, fig. 17

Description.—This species is based on one badly laterally compressed mold of an interior, F. 3837, L. 66, University of New England Collections. Evidently the living chamber is absent, as the specimen is entirely septate.

The conch is elongate in lateral profile, and as an incomplete specimen measures about 50 millimeters high and 39 millimeters wide. Its thickness is difficult to estimate, but it may have been 10 millimeters or more. An accurate transverse profile is quite impossible to determine, but the whorls may have been narrowly rounded ventrally, and compressed laterally (*i.e.*, the lateral parts of the whorls may have been very broadly arched). Umbilical shoulders may have been gently rounded, but the umbilical walls are steep, about normal to the compressed lateral areas of the whorls (since the photograph was taken, the umbilical area has been cleaned free from matrix). The umbilicus is small, about six millimeters in diameter, and decreases at the axis to a small pit about 1.5 millimeters in diameter.

Text-fig. 8 shows the pattern of the external suture, which consists of a trifid ventral lobe (the median portion is much shorter), the flanks of which diverge markedly adorally. Following the ventral lobe is an asymmetrical U-shaped lateral saddle, an acuminate lateral lobe, and a broadly rounded second lateral saddle. The lateral lobe is deeper than the ventral lobe.



TEXT-FIG. 8—Diagrammatric representation of the external suture of *Beyrichoceras* sp. (×1.6). This figure represents the most adoral completely preserved suture.

Camerae are rather short and numerous, approximately eleven in the adoral half-volution.

Remarks.—It is with considerable doubt that this form is referred to *Beyrichoceras*. External ornament is absent (riblike ornament near the umbilicus on fig. 17, pl. 113 is not part of this form), leaving the pattern of the external suture to be the main criterion. The suture pattern drawn is possibly not completely accurate but was taken farthest adorally where the mold is least distorted. Because of the variation is the supposed range of this genus, forms assigned to it must also be given specific assignment for accurate age determination. The paucity of definitely known characters prohibits the assignment of the present form to any species.

Phylum ARACHNOMORPHA Heider, 1913, emend. Størmer, 1944
Subphylum TRILOBITOMORPHA Størmer, 1944
Class TRILOBITA Walch, 1771
?Family PHILLIPSIIDAE Oehlert, 1886

Genus LINGUAPHILLIPSIA Stubblefield, 1948

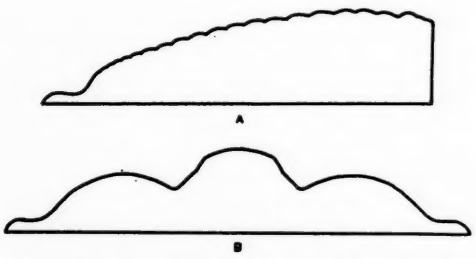
Type species.—Linguaphillipsia terapaiensis Stubblefield, 1948.

Diagnosis.—Phillipsiid; cephalon with flat or gently convex border which becomes wider on free cheek; pre-glabellar field short, usually a border furrow; glabella longer than wide, not expanded anteriorly; sides subparallel to third glabellar furrows, then curving outward and becoming widest at basal lobes; basal furrows strongly curved posteriorly, not necessarily reaching occipital furrow; pygidium with well-defined peripheral area of combined border and border furrow.

Remarks.—Most of the above diagnosis was abstracted from Stubblefield (1948), and the remark on the pygidium added, for the definition of the peripheral area appears to be of generic significance. Perhaps also the relative size and, at least, the position of the eyes could be included in the diagnosis. Shaw (1957, p. 196) believes eye position to be of fundamental importance, citing Lochman (1947, p. 60) and Shaw (1952, p. 465) in support of this.

Specimens of the present study show the generic characters well, except for the palpebral lobes, which Stubblefield says are relatively small. However, this character as quoted from Stubblefield may not be relied on too closely; his figure 3, plate 13 (Stubblefield, 1948) shows a right palpebral lobe which appears relatively large, especially when compared with figures of *Asaphus gemmuliferous* Phillips (Woodward, 1883–1884, pl., 3, figs. 1,2), type species of *Phillipsia* Portlock.

Stubblefield (p. 98) says this genus differs from *Phillipsia* Portlock in the pronounced lateral expansion of the glabella posteriorly. This does not appear to be a diagnostic character, and certain other characters seem much more significant. As emended by Weller (1936) and subsequently revised by Reed (1943), *Phillipsia* Portlock differs from



TEXT-FIG. 9—Longitudinal (A) and transverse (B) sections (×7.3) through the pygidium of *Linguaphillipsia divergens*, n. sp. The transverse section was taken at the greatest width near the anterior margin.

Linguaphillipsia in the following characters: (1) a glabella with the anterior end reaching or nearly reaching the border, (2) smaller eyes, (3) eyes situated further anteriorly, and (4) absence of a well-defined border. Tubercles on the pygidium of *Phillipsia* Portlock may be another differentiating character, but this can not be determined with certainty, since figures of the pygidium of the holotype of *Linguaphillipsia* show only internal molds. It would be expected, however, that if tubercles were present, they could be seen on the internal molds.

At present, the range of this genus appears to be restricted to the Lower Carboniferous. According to Stubblefield, it ranges geographically from Siberia, central and southern Russia to Malaya. This is the first reported occurrence of this genus in Australia.

LINGUAPHILLIPSIA DIVERGENS, n. sp.
Pl. 113, figs. 18–25; text-fig. 9

Diagnosis.—About medium-sized for genus; pre-ocular branches of facial suture very widely divergent; axial lobe of pygidium has 20 axial rings, each pleural lobe with 13 segments; surface smooth.

Types.—Holotype, F. 3562, from 146; partypes, F. 3563A, F. 3563C, F. 3563D, F. 3563F (hypostome) and F. 3563G from L. 146, F. 3564 from L. 148, F. 3565 from L. 66, and F. 3581A–B from L. 146; University of New England Collections.

Material.—F. 3562-F. 3586, including one incomplete cephalon (holotype), five incomplete internal molds of cranidia, and one internal mold of a hypostome, the remainder

being internal and external molds of pygidia, University of New England Collections.

Description.—The cephalon is subsemielliptical, smooth, gently convex longitudinally, and moderately convex transversely. Genal spines are moderately long, extending about one-third the length of the cephalon.

The glabella is gently convex longitudinally and moderately convex transversely. In longitudinal profile, it rises gradually from the front, reaching the maximum convexity about midlength, and then gradually steepens before curving rapidly into the occipital furrow. There are three pairs of lateral furrows. The first or basal furrows are the deepest and strongly curved posteriorly; they partially define the inflated, broadly teardrop-shaped basal lobes. The second pair of furrows is shorter, not so deeply impressed, and slightly curved posteriorly. Third lateral furrows are short and straight, slightly impressed, and slightly pointing posteriorly.

The dorsal furrow delineates the deeply impressed occipital furrow. The occipital ring is asymmetrically convex, appearing in longitudinal section as one-half of a rounded lobe.

Eyes are relatively large, about one-half the length of the glabella (disregarding the occipital ring). Midpoints of the eyes are about at the positions of the basal furrows where they meet the outer edges of the glabella. Surfaces of the eyes are very slightly arched and relatively smooth, so are quite likely holochroal, or covered with a cornea. Facets are hexagonal and very slightly raised. They are very numerous, about 11 within the space of 1 millimeter, and each is about .08 millimeter in diameter. Prominent rounded furrows surround the outer edges of the eyes. Bounding these furrows are prominent subangular shelf-like ridges which extend some distance anterior to the eyes.

Palpebral lobes are relatively large and flexed dorsad at a low angle. Their distal margins form asymmetrical arcs, curved more so posteriorly. No defined palpebral rims are present, and the lobes are shallowly depressed proximally.

The surface of the upturned relatively narrow border is gently convex anteriorly and laterally, becoming less convex towards the genal spines. The relatively wide gently concave border furrow is narrowest just anterior to the glabella, becoming wider laterally. Past the posterior margin the border furrow becomes narrower again as it tapers on the genal spines. The narrower, deeply impressed posterior border furrow is apparently restricted to the free cheeks, separated from the dorsal furrow by low ridges.

Post-ocular branches of the facial suture make a low acute angle with the posterior margin and swing toward the dorsal furrow. Sutures trend a short distance subparallel to the dorsal furrow and then swing outward, approximating the contours of the eyes at their inner edges. Pre-ocular branches swing rapidly outward into wide arcs before reaching the anterior margin at low acute angles.

The hypostome is not unlike, in general form, that figured by Whittington (1954, pl. 2, figs. 21,26,27,32,39 and 44) for *Paladin* (*Paladin*) *helmsensis*. Only an incomplete mold of the interior was found. It had the following measurements (in millimeters; with an approximation made for the missing shell): Length ca. 6.2, width (at anterior wing) ca. 4.4; length from anterior end to posterior border 1.6. The middle body occupies about three-fourths the length of the hypostome. The anterior lobe of the middle body is broadly arched longitudinally, more strongly arched transversely. It is widest at the posterior one-third of the length, tapering towards the front where it ends in a narrowly rounded lobe. The crescent-shaped posterior lobe is about one-fourth the length of the middle body, and separated from the anterior lobe by short posteriorly directed furrows. The posterior lobe is asymmetrically convex in longitudinal profile, more steeply on the posterior slope. Anteriorly, the border is not seen. Anterior wings are seemingly broad and flat, extending upward at the position of the anterior lobe. Lateral borders are apparently narrow, but the broadly convex posterior border is quite long, occupying about one-fourth the length of the hypostome. Shoulders are not pronounced, and the

notch can not be clearly determined. A broadly rounded furrow demarcates the posterior end of the middle body, becoming narrower and deeper laterally before diminishing altogether near the anterior margin of the anterior lobe.

Thoracic segments are unknown except for a few incomplete portions seen on fig. 18, pl. 113.

The pygidium is parabolic in outline, ending posteriorly in a blunt point. It is rather gently convex in both longitudinal and transverse profiles, as shown in text-fig. 9. It is slightly wider than long; the anterior margin extends rather straight out laterally, meeting the curved lateral margin with a sharp, obtuse angle.

The axial lobe is high and has a width between one-third and one-fourth the total width of the pygidium. The crest of the lobe is arched transversely, and the sides of the lobe are straight. A constriction at about mid-height divides the axial lobe throughout its length. There are 20 axial rings separated by well-defined obtusely angular ring furrows, which are poorly defined along the sides of the lobe. The last ring is very short and separated from the preceding ring by a very slightly impressed ring furrow, making it difficult to determine this ring on most specimens. These rings are asymmetrical in longitudinal profile, the steepest side on the posterior slope. The first axial ring is separated by a transverse furrow into a much more convex posterior portion and a less convex anterior portion. A fine, slightly impressed articulating furrow separates the first axial ring from the articulating half ring.

Each pleural lobe has 13 segments, similar in longitudinal profile to the axial rings. However, the most anterior segment is *concave* on the antero-lateral portion. Segmens are poorly defined in the region of the dorsal furrow. There are no apparent subsidiary furrows. In transverse profile (see fig. 9B), the pleural lobe rises outward gradually from the deep dorsal furrow. At about mid-width, the pleural lobe profile plunges more rapidly to the inner edge of the border furrow.

The border is gently convex, separated from the pleural lobe by a relatively wide border furrow, which is widest posterolaterally. This furrow is very slightly concave as it slopes outward from the margin of the pleural lobe. The doublure is gently convex and as wide as the border and border furrow taken together. This structure is bent upward, adjoining the under surface of the shell; it is striate, the striae regular and parallel to the margin.

Measurements.—Designation of measurements is after Shaw (1957, pp. 194–206). All measurements are given in millimeters.

Cephalon

		L. 146		L. 148
Total cephalic length	ca. 9.3	ca. 9.0 (est.)	6.5	8.4
Total spinal-cephalic length	ca. 13.3	—	—	—
Occipital glabellar length	8.0	ca. 7.9 (est.)	5.6	7.4
Total glabellar length	6.6	6.5	4.7	6.2
Exsagittal palpebral length	3.2	ca. 3.0	—	—
Occipital mid-palpebral distance	3.2	ca. 3.0 (est.)	—	—
Maximum cephalic width	ca. 17.0	—	—	—
Palpebral cephalic width	ca. 16.0	—	—	—
Maximum glabellar width	5.4	ca. 4.7	ca. 3.4	ca. 4.0

Pygidium

Maximum Pygidial Width	Anterior Width of Rhachis	Total Length of Rhachis	Total Pygidial Length	Axial	Number of segments Pleural (each pleuron)	Locality
ca. 15 (est.)	4.5	12.0	ca. 13.0	20	13	L. 66
ca. 14.0 (est.)	ca. 3.0	ca. 10.5	ca. 11.0	20	13	L. 66
ca. 13.0	ca. 3.5?	ca. 9.5	ca. 10.5	20?	13	L. 66
ca. 14.0	—0	ca. 10.5	ca. 11.5	20?	13	L. 146
ca. 15.0	4.0	10.0	11.0	20	13	L. 146

Remarks.—Consideration has been given as to whether this species be assigned to "*Phillipsia*" *proxima* Mitchell (1918) (quotation marks added to generic name by the writer) or a new name erected for it. "*P.*" *proxima* is based on a single internal mold of a pygidium from the Lower Carboniferous on the Glen William Road, near Clarencetown, Parish Parr, County Durham, N. S. Wales.

Pygidia of the present species appear indistinguishable from the holotype of "*P.*" *proxima*; however, it would be hazardous to call two forms conspecific solely on pygidia. Also, a portion of the Clarencetown fauna was examined, along with published figures of the funa (Dun, 1902, pls. 21,22 and 23). This revealed that there is no close comparison with Barrington fauna. Although some of the same genera occur in both faunas, *e.g.*, *Leptagonia*, *Rhipidomella*, *Schizophoria*, and *Phricodothyris*, species of these genera are significantly different and separate. Reference of the present species of *Linguaphillipsia* to "*P.*" *proxima* would imply a correlation with Clarencetown, which would be probably erroneous. For stratigraphical reasons, therefore, it seems desirable to erect a new species.

"*Phillipsia*" *elongata* Mitchell (quotation marks added by the writer) from the Lower Carboniferous at Binge Berry (Rouchel Brook) is generally more elongate, has less divergent pre-ocular branches of the facial suture, and wider axial lobe on the pygidium. The type species, *Linguaphillipsia terapaiensis* Stubblefield, has less divergent pre-ocular branches of the facial suture, four pairs of glabellar furrows, and a median tubercle on the occipital ring.

The term border furrow and terminology for the description of the hypostome are that of Whittington & Evitt (1954).

The specific name, *divergens*, refers to the very widely divergent pre-ocular branches of the facial suture.

Occurrence.—To date, this species is known only from the fossiliferous mudstone below the "*Productus*" *barringtonensis* bed from the upper part of the Lower Burindi group, south of Barrington, N. S. Wales; upper Tournaisian.

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EXPLANATION OF PLATE 113

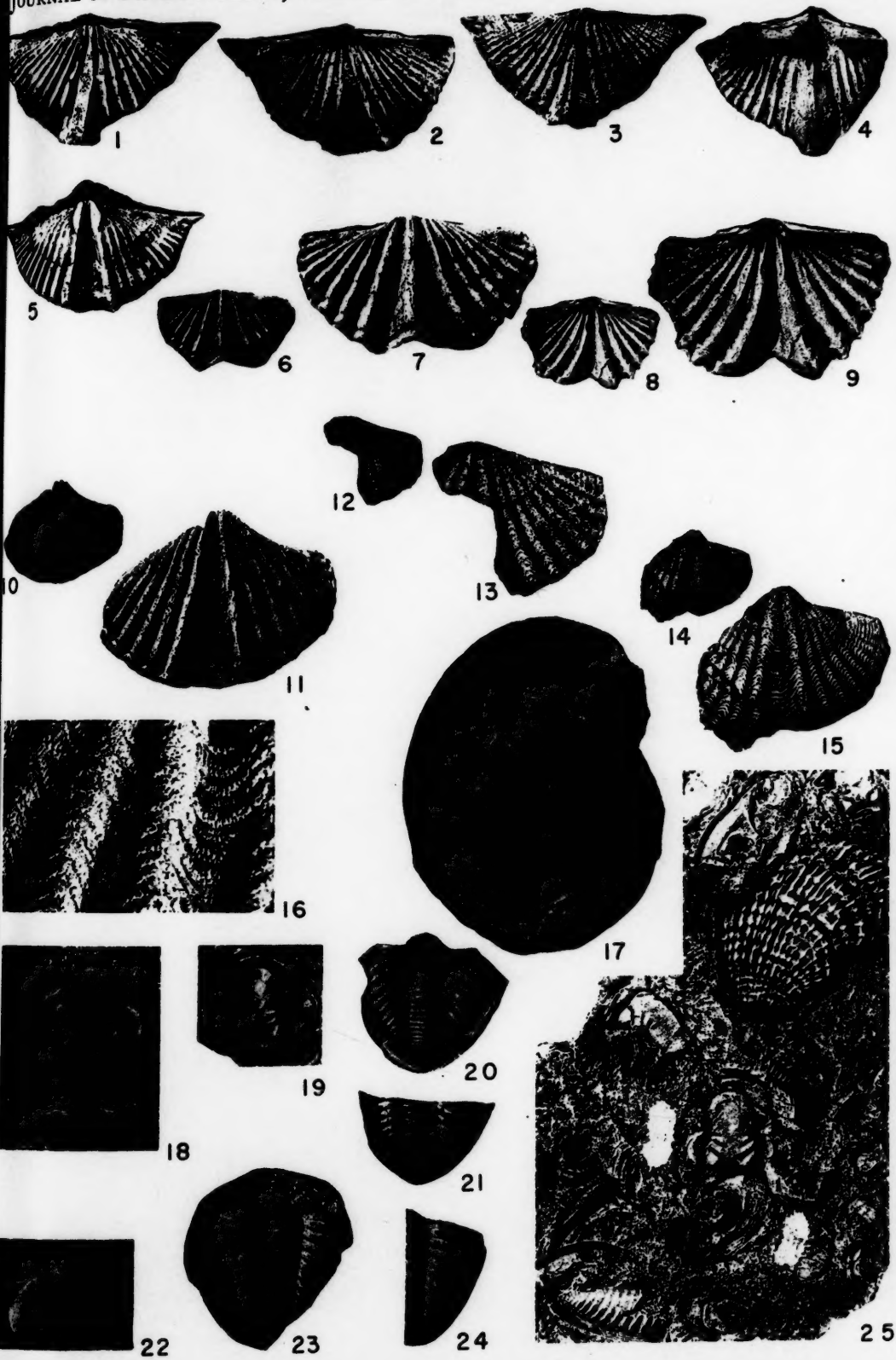
All figures ×1 unless otherwise stated. Specimen numbers F. and collecting locality L. numbers are those of the University of New England.

FIGS. *1–5—Tylothyris planimedia*, n. sp. *1,2,3*, paratype; *1,2*, mold of the brachial interior and rubber cast of same, F. 3392B, and *3*, rubber cast of the exterior, F. 3392A, L. 146; *4*, paratype, rubber cast of the pedicle interior, F. 3395, L. 146; *5*, paratype, pedicle mold of the interior, F. 3394, L. 146.

6–16—Punctospirifer amblys, n. sp. *6,7*, holotype, brachial mold of the interior, ×1 and ×1.8, respectively, F. 3552, L. 66; *8,9*, rubber casts of figs. *6* and *7*, respectively; *10,11*, paratype, pedicle mold of the interior, ×1 and ×1.8, respectively, F. 3550, L. 66; *12,13*, paratype, rubber cast of the brachial exterior, ×1 and ×1.8, respectively, F. 3538B, L. 66; *14,15*, paratype, rubber cast of the pedicle exterior, ×1 and ×1.8, respectively, F. 3551, L. 66; *16*, paratype, portion of a rubber cast of the brachial exterior showing spine bases; slightly anterior to the midlength of the valve; a portion of the median fold is on the extreme right, ×11.5, F. 3533B, L. 145.

17—Beyrichoceras sp. Laterally compressed mold of the interior, ×1.1, F. 3837, L. 66.

18–25—Linguaphillipsia divergens, n. sp. *18*, holotype, cephalon and few thoracic segments, ×1.7, F. 3562, L. 146; *19*, paratype, mold of the interior of the cranidium, ×1.7, F. 3564, L. 148; *20*, paratype, pygidium, ×1.7, F. 3581B, L. 146; *21*, rubber cast of the pygidial exterior, ×1.7, F. 3586B, L. 66; *22*, paratype, mold of the interior of the hypostome, ×3.2, F. 3563F (see also fig. *25f*), L. 146; *23*, paratype, rubber cast of the pygidial exterior, ×1.7, F. 3565, L. 66; *24*, rubber cast of the right lateral portion of the pygidial exterior showing the straight antero-lateral margin, and the concave first anterior segment, ×1.7, F. 3566, L. 66; *25*, rock with several fragmentary trilobite specimens, L. 66; *a*, mold of the exterior of the left free cheek, F. 3563B; *b*, mold of the interior of the cranidium; *c*, mold of the interior of the cranidium, F. 3563C; *d*, paratype, mold of the interior of the cranidium showing the strongly divergent right facial suture, F. 3563D; *e*, mold of the interior of the eye, F. 3563E; *f*, paratype, mold of the interior of the hypostome, F. 3563F; *g*, mold of the interior of the right pygidial pleural lobe showing the striate doublure.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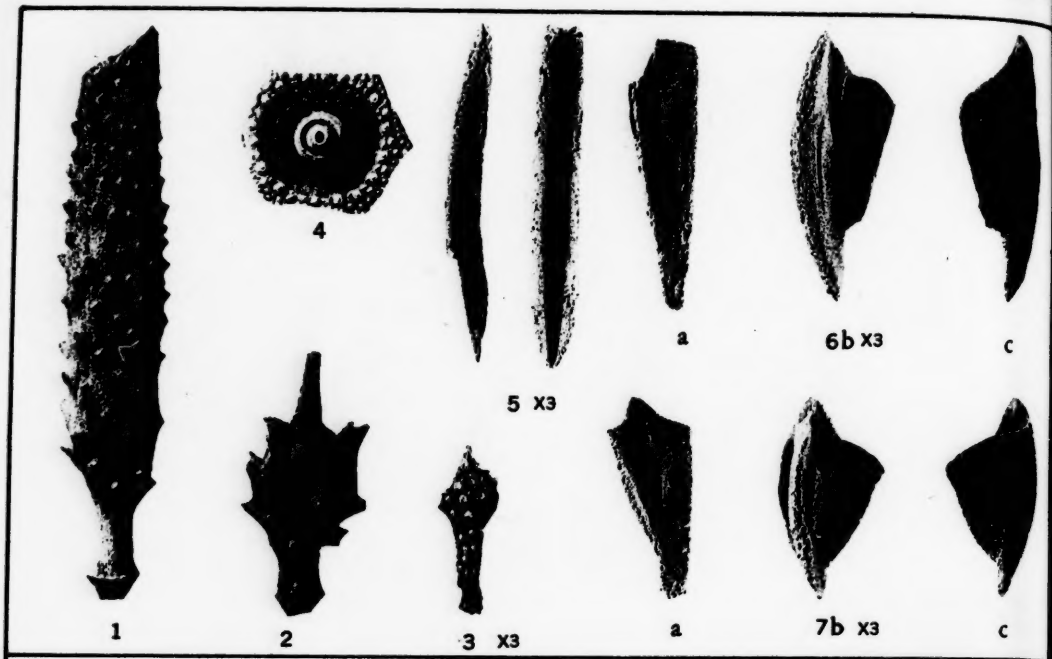
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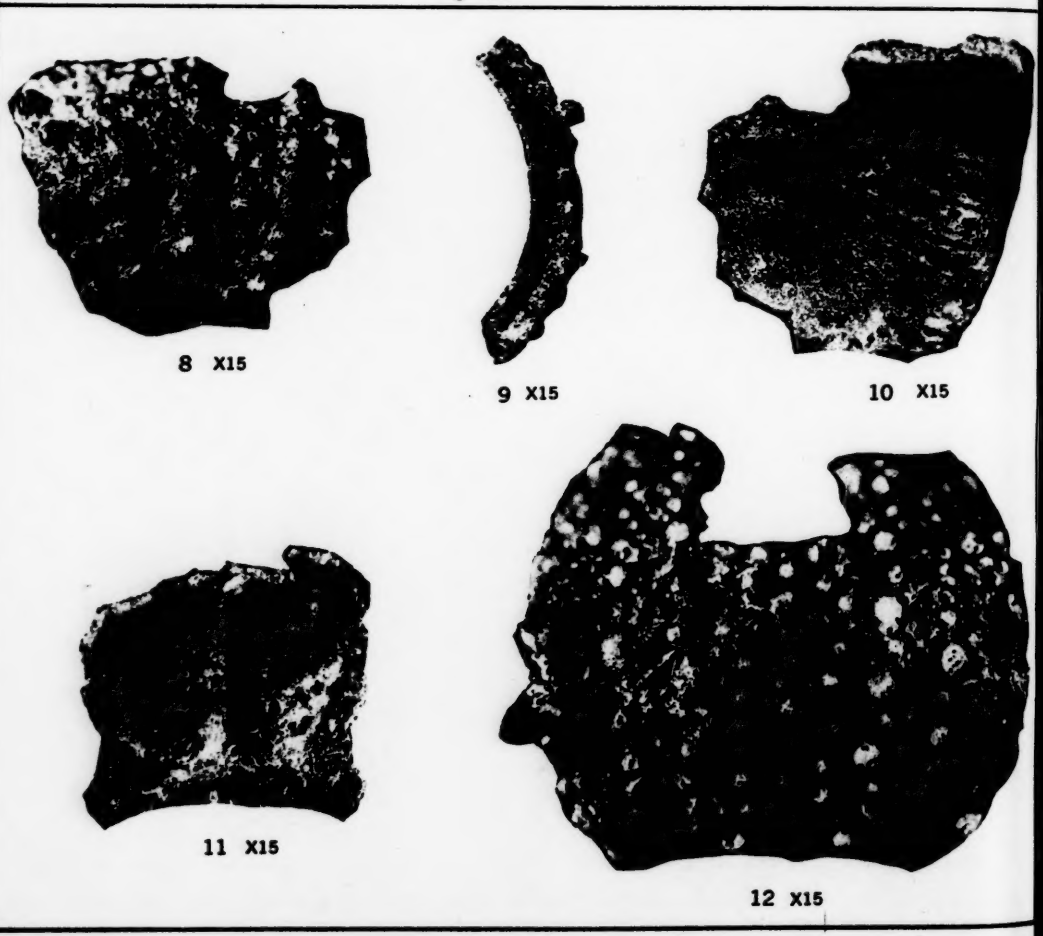
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JOURNAL OF PALEONTOLOGY, V. 32, NO. 5, P. 889–892, PL. 114, 3 TEXT-FIGS., SEPTEMBER 1958

PERMIAN ECHINOIDS FROM WEST TEXAS[1]

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ABSTRACT—A new genus, *Xenechinus*, with type species *X. parvus*, n. sp., is described from the Permian of West Texas. This echinoid is unusual in having one column of plates in each interambulacrum, and covered passageways for the radial vessels. Also described are isolated plates and spines, most of which are cidarid. Two half-pyramids are figured, one with an extremely high angle.

INTRODUCTION

DURING the last nineteen years that Dr. G. Arthur Cooper has been searching through silicified residues from limestones from West Texas, he has found many echinoid fragments. Most of this material consists of spines and isolated plates. He did find, however, twenty-five small fragments of a new and remarkable genus. That he found these fragments, most of which are under 5 mm. in length, and identified them as coming from an echinoid, is a tribute not only to the keenness of his eye but also to his knowledge of echinoids. The discovery of a new Permian echinoid is significant because only two well-authenticated species are known from this period: *Meekechinus elegans* Jackson from the Eskridge shale of Kansas, and *Miocidaris keyserlingi* (Geintz) from Europe.

I thank Richard V. Melville of the Geological Survey of Great Britain and Professor Herbert L. Hawkins of the University of Reading for their opinions on the new species, and Lawrence B. Isham, scientific illustrator, for his skillful reconstruction of the echinoid.

[1] Published by permission of the Secretary of the Smithsonian Institution.

SYSTEMATIC DESCRIPTIONS

Family CRAVENECHINIDAE Hawkins 1946

XENECHINUS, n. gen.

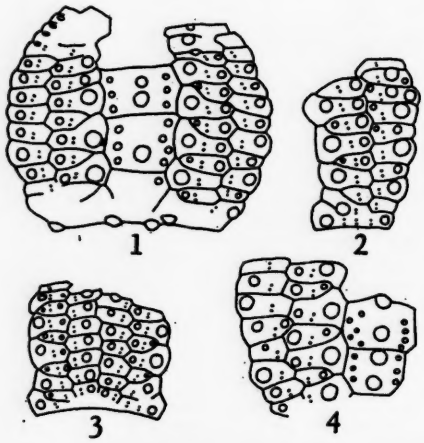
One column in each interambulacrum, four in each ambulacrum, with covered passageways on interior for radial vessel. Test covered with regular series of imperforate tubercles. Plates not imbricate.

Type species.—*Xenechinus parvus*, n. sp.

Discussion.—This genus belongs to the Cravenechinidae because it has uniserial interambulacra, multiserial ambulacra, with adradial columns of large plates with perradially placed pore-pairs. It differs from the other genus in the family, *Cravenechinus* Hawkins, in having four instead of eight columns in each ambulacrum, and imperforate instead of perforate tubercles. The covered passageway for the radial vessel is unusual, having been reported before only in

EXPLANATION OF PLATE 114

FIG. *1*—Spine. USNM 136497, from locality 706b.
2—Spine. USNM 136498, from locality 706c.
3—Secondary spine. USNM 136499, from locality 706b. ×3.
4—Interambulacral plate. USNM 136500, from locality 728.
5—Tooth. USNM 136501, from locality 708u. ×3.
6—Right maxilla—a, outer, b, symphysial, and c, interpyramidal face. USNM 136502, from locality 706b. ×3.
7—Right maxilla—a, outer, b, symphysial, and c, interpyramidal face. USNM 136503, from locality 707e. ×3.
8–12—*Xenechinus parvus*, n. sp. All specimens from locality 701a[3]. *8–10*, exterior, side, and interior views of paratype USNM 136487. ×15. Specimen shows oral portion of interambulacrum and half-ambulacrum. In the side view can be seen the perforations for the podial branches through the covered passageway of the radial vessel. Drawing on text-fig. *2*. *11*, interior view of paratype USNM 136488 showing the oral and ambital portions of an ambulacrum. ×15. *12*, exterior view of holotype USNM 136486 showing two half-ambulacra and included interambulacrum. ×15. Drawing on text-fig. *1–1*.



TEXT-FIG. *1*—*Xenechinus parvus*, n. sp. All figures ×8. (1) Holotype USNM 136486 (photograph, pl. 114, fig. 12), (2) Paratype USNM 136505, (3) Paratype USNM 136488 (photograph pl. 114, fig. 11), (4) Paratype USNM 136487 (photograph, pl. 114, fig. 8).

the Ordovician genera *Aulechinus* and *Ectinechinus*. This structure in *Xenechinus* differs from that of the Ordovician genera in being adapted to a rigid test.

XENECHINUS PARVUS, n. sp.
Pl. 114, figs. 8–12, text-figs. 1–3

Material.—The collection contains twenty-three silicified fragments probably representing from six to eight different individuals. The holotype (pl. 114, fig. 12) is the largest of the fragments, with two-thirds of the length from the peristome aborally consisting of one interambulacrum and its two adjacent half ambulacra. Paratype 136488 (pl. 114, fig. 11) preserves the oral portion of an ambulacrum and displays the covered passageway for the radial vessel. Paratype 136505 (text-fig. 1–2) is the oral portion of a half-ambulacrum, and paratype 136487 (pl. 114, figs. 8–10) the oral portion of an interambulacrum and half-ambulacrum with the grooves from the covered passageway to the pore-pairs particularly clear.

Shape.—Test high, with flat oral surface, Species, small, holotype with estimated horizontal diameter of 9–10 mm.

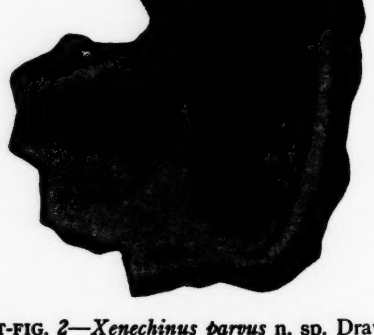
Ambulacra.—Wide, three times width of interambulacra, with four columns in each area. At midzone, alternate plates of outer columns greatly enlarged in adradial portions of plates, separating adjacent plates in same column from adradial suture; three or four occluded plates in each column. Plates of inner columns regular primaries, with approximately twenty plates in a column, two and one-half plates to each interambulacral plate. Pore-pairs in peripodia on inner margin of adradial plates, outer margin of plates of inner columns with pores of pairs almost vertically superimposed, upper pore nearer adradial suture. On oral margin, six pore-pairs in series instead of usual four; character of plates not clear because sutures not visible. On interior, (pl. 114, figs. 10,11) pore-pairs nearly horizontal with outer pore slightly aboral to inner pore; outer pore passing straight through test, inner pore obliquely. Pores at base of arch (pl. 114, fig. 9) passing from radial vessel to inner pore of pore-pair.

Interambulacra.—Narrow, single column in each area with six to eight plates in each column. Plates irregularly square, thickened along transverse suture. Column separated from peristome by ambulacral plates.

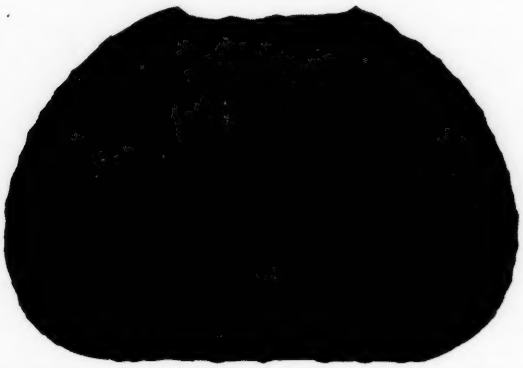
Peristome.—Large, diameter one-half horizontal diameter of test.

Apical system.—Unknown.

Tuberculation.—Test covered with regular



TEXT-FIG. *2*—*Xenechinus parvus* n. sp. Drawing by Lawrence B. Isham of paratype USNM 136487 showing grooves leading from the covered passageway, for the radial vessel, to the pore-pairs. ×15.



TEXT-FIG. 3—*Xenechinus parvus*, n. sp. Reconstruction of test. Character of plates and shape of test above midzone not known but probably similar to that shown in reconstruction. Drawing by Lawrence B. Isham. ×8.

series of imperforate tubercles. Largest tubercles on interambulacral plates, usually two on each plate, each near transverse suture; six to eight smaller tubercles in longitudinal series along adradial suture. Four longitudinally-arranged series on ambulacra along adradial margin of outer column, also on perradial margin of inner column. Tubercles on inner margin of outer column smaller.

Types.—Holotype, USNM 136486; paratypes USNM 136487–8, 136505.

Horizon and locality.—Permian, Wolfcamp formation, locality 701a[3] (see locality data below).

ECHINOID FRAGMENTS

Most of the echinoid fragments come from the Word formation (locality 706b-c). There are over 150 spines, and most of them can be divided into three types. The largest (pl. 114, fig. 1) is tapering and has a maximum length over 90 mm; the second (pl. 114, fig. 2) shorter, with a maximum length of 50 mm. and is expanded, and the third (pl. 114, fig. 3) is very small, mace-shaped, with a maximum length of 18 mm. Probably all these spines came from the same species, with the longest spines attached at the ambital region, shorter, aborally and orally, and smallest, secondary. As all the spines are spinulated, the echinoid must have been a cidarid.

Most of the isolated plates are interambulacral, and from a cidarid as shown by their well-developed perforated primary tubercles (pl. 114, fig. 4). Spines and plates identical with these also occur from the Guadalupian (locality 728).

The few cidarid plates and spines from other localities, can be easily distinguished from the ones described above. From locality 701a[3] there are several lephesthid ambulacral plates. Several half-pyramids and teeth (pl. 114, fig. 5) are in the collection with one half-pyramid (pl. 114, fig. 6) being of particular interest because of its extremely low angle. Having a very shallow foramen magnum this pyramid probably came from a cidarid. No other Paleozoic pyramid with as low an angle has been described; the most erect lantern hitherto described belongs to *Lepidechinoides hunti* Cooper.

In conclusion, most of the echinoid fragments are cidarid except for a few lepidesthid plates and fragments of *Xenechinus parvus*.

HORIZONS AND LOCALITIES

701a[3]—Wolfcamp formation (bed 9 of Cooper). From limestone block on slope just south of forks of canyon, 0.4 mile N81° W of hill 5060; Wolf Camp Hills, Hess Canyon Quadrangle, Texas.

706b—Word formation (between limestone no. 3 and limestone no. 4). Limestone in upper part of Word, 0.2 mile west of junction of Hess Canyon with south branch of Hess Canyon, Hess Canyon Quadrangle, Texas.

706c—Word formation (about middle of limestone no. 2) southwest slope and crest of low hill 3.7 miles N 36° E (airline) of Hess ranch house, Hess Canyon Quadrangle, Texas.

707e—Word (Lower). 5.3 miles (airline) N 5° W of Decie Ranch house, 0.9 mi (airline) S 25° E of Sullivan Peak, on nose of foothill southeast of Sullivan Peak, Altuda Quadrangle, Texas.

708u—Leonard formation. Loose pieces on south slope of gully, 2.0 mi. N 65° E of Split Tank, Hess Canyon Quadrangle, Texas.

728—Guadalupian (Cherry Canyon formation—Getaway member). From lens near break in slope on middle leader on the west side of airway station road, between highway and pipeline road, on crest of the ridge. Airway station is between Pine Spring Camp and El Capitan, Quadalupe Mountains, 2½ miles by road southwest of Pine Spring Camp, Guadalupe Peak Quadrangle, Texas.

LITERATURE CITED

HAWKINS, H. L., 1946, *Cravenechinus*, a new type of echinoid from the Carboniferous Limestone: Geol. Mag. London, v. 83, p. 192–197, fig. 1, pl. 13.

MANUSCRIPT RECEIVED FEBRUARY 24, 1958.

JOURNAL OF PALEONTOLOGY, V. 32, NO. 5, P. 893–906, PLS. 115–117, SEPTEMBER 1958

SHUMARD'S TYPE SPECIMENS OF TERTIARY MOLLUSKS FROM OREGON AND OTHER TYPES FORMERLY AT WASHINGTON UNIVERSITY, ST. LOUIS*

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U. S. Geological Survey, Washington, D. C.

ABSTRACT—The entire type collection of invertebrates and vertebrates formerly in the Department of Geology and Geological Engineering at Washington University, St. Louis, Missouri, is now on permanent deposit in the U. S. National Museum. Nine holotypes include a brachiopod and a gastropod of Paleozoic age, Paleozoic and Cretaceous cephalopods and echinoids, and the holotype of *Palaeotherium(?) proutii* (=*Menodus proutii*) Owen, Norwood, & Evans, the first titanothere to be illustrated. There are 20 syntypes, 4 lots of paratypes, and 35 lots of figured specimens. Three lectotypes of Tertiary pelecypods and the lectotype of a Devonian brachiopod are here designated. These types are listed according to their biologic group and age assignment; the list includes type designations, references, locality data, and U. S. National Museum catalogue numbers.

In 1858, B. F. Shumard, described, but did not illustrate, 6 species of pelecypods from the Tertiary of Oregon. The type specimens of 3 of these species (*Leda oregona*, *Pecten coosensis*, and *Venus securis*) are recognized in the Washington University type collection and are redescribed and illustrated. The type specimens of *Leda willamettensis*, *Lucina fibrosa*, and *Corbula evansana* seem to be lost.

INTRODUCTION

IN THE fall of 1956 the late Dr. James Steele Williams informed me that some of Shumard's types were on deposit in the Department of Geology and Geological Engineering at Washington University, St.Louis, Missouri. I am deeply indebted to Dr. Williams for this information; it led both to the gift to the U. S. National Museum of Washington University's entire type collection of invertebrates and vertebrates, and to the locating of the types of 3 of Shumard's 6 Tertiary pelecypods from Oregon. The gift of the type collection was made possible through the kindness and farsightedness of Drs. Courtney Werner, Carl Tolman, and N. S. Hinchey of the Department of Geology and Geological Engineering, Washington University.

THE TYPE COLLECTION

Table 1 is a list of the type specimens, giving the names, ages, and locality data as they appeared in the publications listed. Corrections and additions to the original information are bracketed. The specimens under consideration have been assigned U. S. National Museum catalogue numbers in the appropriate catalogue books, and these numbers are included in the table.

A specimen is listed as a holotype if it was illustrated by the original author and agrees with the illustration. If a specimen does not agree exactly with the original illustration or description, it is listed as "holotype?"; and it is so listed, also, if there is only one specimen and no original illustration, and it cannot be proved that the specimen is the holotype. It is for specialists to determine the status of these specimens. If there are 2 or more specimens, all illustrated, or if none is illustrated or designated the type, the specimens are listed as syntypes. The specimens listed as lectotypes are designated as such in the systematic descriptions in this paper, with the exception of *Atrypa snyderensis* Greger, for which a lectotype is designated in Table 1. A lectotype has been designated for *Atrypa snyderensis*, at the suggestion of G. A. Cooper (oral communication), because the specimen concerned is by far the best in the lot and the obvious choice for the lectotype, and has written on it in ink the work "Holotype," below which are initials that seem to be Greger's. The specimens remaining in the type lot from which a lectotype has been selected are listed as paratypes.

* Publication authorized by the Director, U. S. Geological Survey.

Of particular interest in this collection are the holotypes of species originally described by Shumard, White, or Owen, Norwood, & Evans, most of which have been supposed for decades to be lost.

The preparation of the table has been made possible by the generous help of my colleagues in the U. S. Geological Survey and the U. S. National Museum. I wish especially to acknowledge the assistance of G. A. Cooper, C. L. Gazin, and P. M. Kier of the U. S. National Museum and the late J. B. Reeside, Jr., Helen Duncan, and J. M. Berdan of the U. S. Geological Survey.

SHUMARD'S TERTIARY MOLLUSK TYPES FROM OREGON

B. F. Shumard (Professor at Bonham's Seminary in St. Louis) in 1858 (p. 120–123) described but did not illustrate 6 species of pelecypods from the Tertiary of Oregon, which he named *Leda willamettensis*, *Leda oregona*, *Pecten coosensis*, *Lucina fibrosa*, *Venus securis*, and *Corbula evansana*. The type specimens of these species have been listed in subsequent papers as missing or lost. The types of *Leda oregona*, *Pecten coosensis*, and *Venus securis* have been recognized in the Washington University collection. The types of *Lucina fibrosa*, *Corbula evansana*, and *Leda willamettensis* are still presumed to be lost. The types of *Inoceramus vancouverensis*, *Pinna calamitoides*, and *Pyrula glabra* from the Cretaceous of Nanaimo River, Vancouver Island, described by Shumard in the same paper (p. 123–125), have not been located and also are presumed to be lost.

The generic and specific features of the 6 Tertiary species of Shumard have been imperfectly known. The original descriptions were brief and not accompanied by illustrations, yet his names have been used by paleontologists for the last 50 years. *Leda oregona* is an Oligocene *Yoldia* that was originally collected near Salem, Oregon. *Pecten coosensis* is a *Patinopecten*, and *Venus securis* is a *Chione* of the subgenus *Securella;* both were originally collected in Oregon from the Empire formation, of Pliocene(?) age.

I am indebted to Prof. E. F. Lange of Portland State College, Oregon, for information concerning the year when Dr. Evans probably collected the specimens from Oregon described by Shumard.

SYSTEMATIC DESCRIPTIONS

Class PELECYPODA

"LEDA WILLAMETTENSIS" Shumard, nomen dubium

Leda willamettensis Shumard, 1858, p. 121, (reprinted in Dall, 1909, p. 187). Gabb, 1869, p. 122. Dall, 1909, p. 104,187.

Nuculana willamettensis (Shumard). Grant & Gale, 1931, p. 126. Weaver, 1942 (1943), p. 41–42.

A single broken sandstone cast of the interior of a double-valved specimen is labeled "*Yoldia willamettensis* (Shumard)". This specimen (pl. 115, fig. 2) is here considered to be *Yoldia* (*Kalayoldia*) *oregona* (Shumard), USNM 567471. The specimen agrees with the original description of *Y.* (*K*). *oregona* and not with the original description of "*Leda willamettensis.*"

The locality description given by Shumard for "*Leda willamettensis*" is "Occurs . . . in dark-gray siliceous limestone, at Brook's Lime Quarry, Willamette Valley, five miles north of Salem, Oregon Territory." The locality given on the specimen labeled "*Yoldia willamettensis*" is "Tertiary, Miocene, Empire formation, Eugene City, Oreg., E. & S. Coll." The label is not in Shumard's handwriting, and in addition, the rock of which the cast is composed is not a "dark-gray siliceous limestone", but a buff tuffaceous sandstone like the matrix of *Yoldia* (*Kalayolidia*) *oregona*.

The original description of "*Leda willamettensis*" could apply to a *Nuculana;* the fact that Shumard said the shell was small might exclude it from *Yoldia*. Shumard's species may be related to *Nuculana washingtonensis* (Weaver) (1916, p. 34–35, pl. 3, figs. 25,26) which has been recorded by Baldwin, Brown, Gair, & Pease (1955) as coming from a tuffaceous sandstone unit of middle Oligocene age, shown on their map northwest of Salem, Oregon.

The original description of "*Leda willamettensis*" is brief and not accompanied by an illustration, and the type specimen is presumably lost. The generic assignment is therefore uncertain, and this name is considered a *nomen dubium*.

TABLE 1.—TYPE SPECIMENS FORMERLY AT WASHINGTON UNIVERSITY, ST. LOUIS, NOW ON DEPOSIT IN THE U. S. NATIONAL MUSEUM

Invertebrates	Status	Reference	Locality	USNM Catalogue Number	Number of Specimens
Brachiopods:					
Coal Measures [Permian?]:					
Spirifer organensis Shumard	Syntypes	Shumard, 1863, p. 108. [Fig'd by Greger, 1932, p. 131, pl. 12, figs. 1–4]	Near Ft. Filmore, Organ Mountains, New Mexico. [Misspelled "Oregon Mountains" in text; "Organ Mts." on original label. Greger, 1932, p. 130, "Pennsylvanian . . . Organ Mountains northeast of . . . Mesquite, Doña Ana County, New Mexico"]	135226	4
Coal Measure Strata [Pennsylvanian]:					
Productus costatus Sowerby var.	Figured specimen	White, 1881, p. 516–517, pl. 8, figs. 7,8	Silver Mine, Vermillion Co., Indiana	135215	1
Spirifer cameratus Morton	Figured specimen	White, 1881, p. 517–518, pl. 8, fig. 3	Waterman, Parke Co., Indiana	135216	1
Spirifer (Martinia) lineatus Martin	Figured specimen	White, 1882, p. 372–373, pl. 42, figs. 4–6	Eugene, Indiana. [Label reads, "Newport, Vermillion Co., Indiana"]	135223	1
Productus punctatus Martin	Figured specimen	White, 1882, p. 373, pl. 42, figs. 1–3	Newport, Indiana	135224	1
Sub-Carboniferous Series [Mississippian]:					
Spirifer textus Hall	Figured specimen	White, 1881, p. 512–513, pl. 7, figs. 1,2	Knobstone division, near Providence and New Albany, Indiana	135212	1
Mississippian:					
Strophalosia orbiculata Hinchey & Ray	Figured syntype	Hinchey & Ray, 1935, p. 248–249, pl. 25, fig. 1	Warsaw formation, ¼ mile south of Osage Hills station on St Louis and San Francisco Railroad, St. Louis Co., Missouri	136332 [Wash. Univ. number 730001]	1
Strophalosia orbiculata Hinchey & Ray	Figured syntype	Hinchey & Ray, 1935, p. 248–249, pl. 25, fig. 2	Same locality as above	136333 [Wash. Univ. number 730001]	1
Strophalosia orbiculata Hinchey & Ray	Figured syntype	Hinchey & Ray, 1935, p. 248–249, pl. 25, fig. 3	Same locality as above	136334 [Wash. Univ. number 730001]	1
Strophalosia orbiculata Hinchey & Ray	Figured syntype	Hinchey & Ray, 1935, p. 248–249, pl. 25, figs. 4,5	Same locality as above	136335 [Wash. Univ. number 730001 in text, 730002 in vial.]	1
Strophalosia orbiculata Hinchey & Ray	Figured syntype	Hinchey & Ray, 1935, p. 248–249, pl. 25, figs. 6,7	Same locality as above	136336 [Wash. Univ. number 730001]	1
Strophalosia orbiculata Hinchey & Ray	——	Hinchey & Ray, 1935, p. 248–249	Same locality as above	136357 [Wash. Univ. number 730001]	1
Strophalosia subelliptica Hinchey & Ray	Figured syntype	Hinchey & Ray, 1935, p. 249, pl. 25, fig. 8	Warsaw formation, on concrete highway (Antire road) 300 yards east of bridge over Meramec River, St. Louis Co., Missouri	136337 [Wash. Univ. number 730002]	1
Strophalosia subelliptica Hinchey & Ray	Figured syntype	Hinchey & Ray, 1935, p. 249, pl. 25, figs. 9,10	Same locality as above	136338 [Wash. Univ. number 730002]	1
Strophalosia subelliptica Hinchey & Ray	Figured syntype	Hinchey & Ray, 1935, p. 249, pl. 25, fig. 11	Same locality as above	136339 [Wash. Univ. number 730002]	1
Strophalosia fortispinosa Hinchey & Ray	Figured syntype	Hinchey & Ray, 1935, p. 249–250, pl. 25, figs. 13,14	Warsaw formation, ¼ mile south of Osage Hills station on St. Louis and San Francisco Railroad, St. Louis Co., Missouri	136340 [Wash. Univ. number 730004]	1
Strophalosia fortispinosa Hinchey & Ray	Figured syntype	Hinchey & Ray, 1935, p. 249–250, pl. 25, fig. 15	Same locality as above	136341 [Wash. Univ. number 730004]	1

TABLE 1—*Continued*

Invertebrates	Status	Reference	Locality	USNM Catalogue Number	Number of Specimens
Strophalosia fortispinosa Hinchey & Ray	Figured syntype	Hinchey & Ray, 1935, p. 249–250, pl. 25, figs. 16,17	Same locality as above	136342 [Wash. Univ. number 730004]	1
Strophalosia fortispinosa Hinchey & Ray	Figured syntype	Hinchey & Ray, 1935, p. 249–250, pl. 25, fig. 18	Same locality as above	136343 [Wash. Univ. number 730004]	1
Strophalosia fortispinosa Hinchey & Ray	Figured syntype	Hinchey & Ray, 1935, p. 249–250, pl. 25, fig. 19	Same locality as above	136344 [Wash. Univ. number 730004]	1
Strophalosia fortispinosa Hinchey & Ray	Figured syntype	Hinchey & Ray, 1935, p. 249–250, pl. 25, fig. 20	Same locality as above	136345 [Wash. Univ. number 730004]	1
Strophalosia fortispinosa Hinchey & Ray	Figured syntype	Hinchey & Ray, 1935, p. 249–250, pl. 25, fig. 21	Same locality as above	135346 [Wash. Univ. number 730004]	1
Strophalosia fortispinosa? Hinchey & Ray	———	Hinchey & Ray, 1935, p. 249–250	Same locality as above	136347 [Wash. Univ. number 730004]	6
Strophalosia fortispinosa? Hinchey & Ray	———	Hinchey & Ray, 1935, p. 249–250	Warsaw formation, on concrete highway (Antire road) 300 yards east of bridge over Meramec River, St. Louis Co., Missouri	136348 [Wash. Univ. number 730004]	1
Strophalosia sp.	Figured specimen	Hinchey & Ray, 1935, p. 250, pl. 25, fig. 12	Same locality as above	136349 [Wash. Univ. number 730003]	1
Strophalosia sp. indet.	———	———	Same locality as above	136350 [Wash. Univ. number 730137]	3
Strophalosia sp. indet.	———	———	Same locality as above	136351 [Wash. Univ. number 730136]	4
Strophalosia sp.	———	———	Warsaw formation, ¼ mile south of Osage Hills station on St. Louis and San Francisco Railroad, St. Louis Co., Missouri	136352 [Wash. Univ. number 730138]	10 [Including fragments]
Devonian:					
Spirifer acuminata Conrad	Figured specimen	White, 1881, p. 503–504, pl. 4, figs. 1–3	North Vernon, Indiana	135211	1
Gruenewaldtia gregeri (Rowley)	Figured specimens	Greger, 1936a, p. 94–95, pl. 1, figs. 1–6,11,13	Snyder Creek shale, Calaway Co., Missouri. [On label, "6 mi. S. of Fulton, type locality"]	135187	6
Gruenewaldtia latilinguis (Schnur)	Figured specimen	Greger, 1936a, p. 94, pl. 1, figs. 14–16	Eifelien, Bensberg, Eifel, Germany	135188	1
Atrypa missouriensis Miller	Figured specimens	Greger, 1936b, p. 43–47, pl. 1, figs. 1–16	Callaway limestone, near Bellama Springs, Callaway Co., Missouri	135189	16
Atrypa missouriensis Miller	Figured specimens	Greger, 1936b, p. 43–47, pl. 2, figs. 1–6	East of Otterville, Cooper Co., Missouri	135190	4
Atrypa planosulcata Webster	Figured specimens	Greger, 1936b, p. 47, pl. 2, figs. 7–12. [Specimen for fig. 12 missing?]	Snyder Creek shale, Strophonella zone. [On label, "6 mi. S. of Fulton, Mo."]	135191	4
Atrypa devoniana Webster	Figured specimens	Greger, 1936b, p. 48, pl. 3, figs. 1–5	Snyder Creek shale, Missouri. [On label, "6 mi. S. of Fulton, Mo."]	135192	4
Atrypa rockfordensis Webster	Figured specimens	Greger, 1936b, p. 48–51, pl. 3, figs. 6–8	Snyder Creek shale, Missouri. [On label, "6 mi. S. of Fulton, Mo."]	135193	3
Atrypa callawayensis Greger	Holotype	Greger, 1936b, p. 51–52, pl. 3, figs. 9–11	Snyder Creek shale, Strophonella zone, Missouri. [On label, "Snyder Creek, Callaway Co."]	135194	1

TABLE 1—*Continued*

Invertebrates	Status	Reference	Locality	USNM Catalogue Number	Number of Specimens
Atrypa snyderensis Greger	Lectotype [No type designation in text]	Greger, 1936b, p. 52, pl. 4, fig. 1, ["Holotype" written in ink on specimen fig'd pl. 4, fig. 1. This specimen is designated the lectotype at the suggestion of G. A. Cooper, oral communication]	Upper Snyder Creek, Missouri. [On label, "6 mi. S. of Fulton"]	135195	1
Atrypa snyderensis Greger	Paratypes	Greger, 1936b, pl. 4, figs. 1–3,5	Upper Snyder Creek, Missouri. [On label, "6 mi. S. of Fulton"]	135196	4
Upper Silurian [Middle Silurian]:					
Rhynchonella tennesseensis Roemer	Figured specimen	White, 1881, p. 496–497, pl. 3, figs. 2–4	Niagara group, near Waldron, Decatur Co., Indiana	135209	1
Spirifer radiata Sowerby	Figured specimen	White, 1881, p. 497, pl. 3, figs. 5,6	Niagara group, near Waldron, Indiana	135120	1
Upper Ordovician:					
Hesperorthis tricenaria (Conrad)	Figured specimens	Greger & Born, 1936, p. 73, pl. 1, figs. 1–3	Valmeyer, Illinois	135197	2
Dinorthis proavitus Winchell and Schuchert	Figured specimens	Greger & Born, 1936, p. 73, pl. 1, figs. 4–6	Valmeyer, Illinois	135198 a & b	2
Dinorthis proavitus Winchell and Schuchert	———	Greger & Born, 1936, p. 73	Valmeyer, Illinois	135198 c	1
Hebertella insculpta (Hall)	Figured specimens	Greger & Born, 1936, p. 73, pl. 1, figs. 7–9. [Specimen for fig. 7 missing?]	Valmeyer, Illinois	135199	2
Rhipidomella tersa (Sardeson)	Figured specimens	Greger & Born, 1936, p. 73, pl. 1, figs. 10–12	Valmeyer, Illinois	135200	2
Plaesiomys subquadratus (Hall)	Figured specimens	Greger & Born, 1936, p. 73, pl. 1, figs. 13,14	Valmeyer, Illinois	135201	2
Strophomena odessae Bassler	Figured specimens	Greger & Born, 1936, p. 73, pl. 2, figs. 1,2	Valmeyer, Illinois	135202	2
Sowerbyella saxeus (Sardeson)	Figured specimens	Greger & Born, 1936, p. 73, pl. 2, figs. 3,4	Valmeyer, Illinois	135203	3
Leptaena unicosta Meek and Worthen	Figured specimens	Greger & Born, 1936, p. 73 ,pl. 2, figs. 6,7	Valmeyer, Illinois	135204	2
Vellamo americanus (Whitfield)	Figured specimen	Greger & Born, 1936, p. 73, pl. 2, figs. 8,9	Valmeyer, Illinois	135205	1
Platystrophia foerstei McEwan	Figured specimens	Greger & Born, 1936, p. 73, pl. 2, figs. 10,11	Valmeyer, Illinois	135206	2
Rhynchotrema capax (Conrad)	Figured specimens	Greger & Born, 1936, p. 73, pl. 2, figs. 12–14	Valmeyer, Illinois	135207	5
Rhynchotrema manniense Foerste	Figured specimen	Greger & Born, 1936, p. 73, pl. 2, fig. 15	Valmeyer, Illinois	135208	1
Pelecypods:					
Miocene [Pliocene]:					
Pecten coosensis Shumard	Lectotype	Shumard, 1858, p. 122	Mouth of Coose [Coos] Bay, Oregon	562472	1
Pecten coosensis Shumard	Paratypes	Shumard, 1858, p. 122	Mouth of Coose [Coos] Bay, Oregon	562473	2
Venus securis Shumard	Lectotype	Shumard, 1858, p. 122–123	Mouth of Coose [Coos] Bay, at Cape Blanco, and on the shores of the Columbia River near Astoria, Oregon. [The lectotype probably came from Coos Bay but might have been collected at Cape Blanco. The type locality is restricted to Coos Bay, Oregon]	562474	1

TABLE 1—*Continued*

Invertebrates	Status	Reference	Locality	USNM Catalogue Number	Number of Specimens
Venus securis Shumard	Paratypes	Shumard, 1858, p. 122–123	Mouth of Coose [Coos] Bay, at Cape Blanco, and on the shores of the Columbia River near Astoria, Oregon. [None of these specimens could have been collected near Astoria, Oregon]	562475	8
Miocene [Oligocene]:					
Leda oregona Shumard	Lectotype	Shumard, 1858, p. 121–122	Willamette Valley, a few miles south of Oregon City, Oregon	562470	1
Leda oregona Shumard [Labeled "*Yoldia willamettensis* (Shumard)".]	Paratype?	Shumard, 1858, p. 121–122	[Labeled "Tertiary, Miocene, Eugene City, Oreg."]	562471	1
Cretaceous:					
Pecten quadricostatus Sowerby	[Specimen discussed by Shumard?]	Shumard, 1853, p. 191, "pl. —, fig. —." [Not the specimen fig'd in pl. 3, fig. 6]	Fort Washita. [Northwestern Bryan Co., Oklahoma]	129188	1
Coal Measures [Pennsylvanian]:					
Allorisma subcuneata Meek and Hayden?	Figured specimen	White, 1881, p. 518–519, pl. 8, figs. 1,2	Edwardsport, Knox Co., Indiana	135217	1
Nucula ventricosa Hall	Figured specimen	White, 1882, p. 371–372, pl. 42, figs. 9,10	Sullivan Co., Indiana	135222	1
Gastropods:					
Coal Measures [Pennsylvanian]:					
Polyphemopsis fusiformis Hall	Figured specimen	White, 1881, p. 519, pl. 8, fig. 6	Newport, Indiana	135218	1
Pleurotomaria tabulata Hall	Figured specimen	White, 1881, p. 519–520, pl. 8, figs. 4,5	Rush Creek, Posey Co., Indiana	135219	1
Sub-Carboniferous [Mississippian]:					
Platyceras equilatera Hall	Figured specimen	White, 1881, p. 514, pl. 7, fig. 5	Keokuk division, Crawfordsville, Indiana	135213	1
Bellerophon sublaevis Hall	Figured specimen	White, 1882, p. 359–360, pl. 40, figs. 5–7	Warsaw division, Ellettsville, Monroe Co., Indiana	135220	1
Chouteau limestone [Mississippian]:					
Chemnitzia tenuilineata Shumard	Holotype? [Specimen does not agree with pl. C, fig. 12]	Shumard, 1855, p. 207, pl. C, fig. 12	Cooper Co., Missouri	135228	1

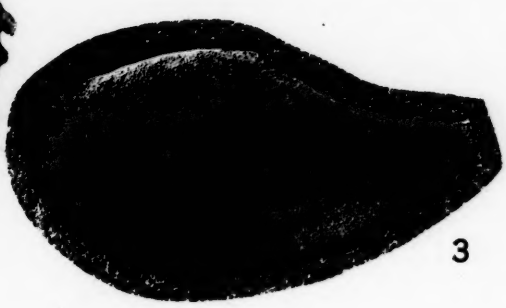
EXPLANATION OF PLATE 115

FIGS. *1,4—Patinopecten coosensis* (Shumard). *1*, right valve of immature specimen, Empire formation, Pliocene(?), Coos Bay, Oregon, USNM 107791, ×1½; *4*, right valve, showing grooved ribs, USGS 2954, Empire formation, Pliocene(?), Coos Bay, Oregon, USNM 107791, ×1.

2,3—Yoldia (Kalayoldia) oregona (Shumard). *2*, paratype?, right valve of cast of interior of double-valved specimen, Oligocene, Eugene, Oregon, USNM 562471, ×1½. *3*, lectotype, external impression in sandstone, showing faint concentric lines, Willamette Valley, Oligocene, a few miles south of Oregon City, Oregon, USNM 562470, ×1½.

1

2



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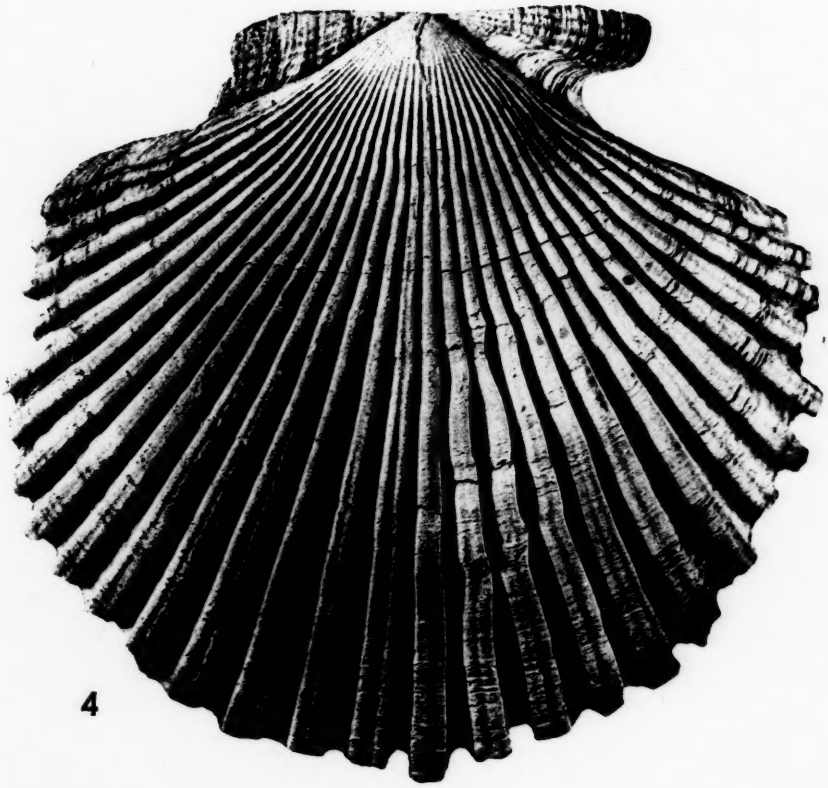

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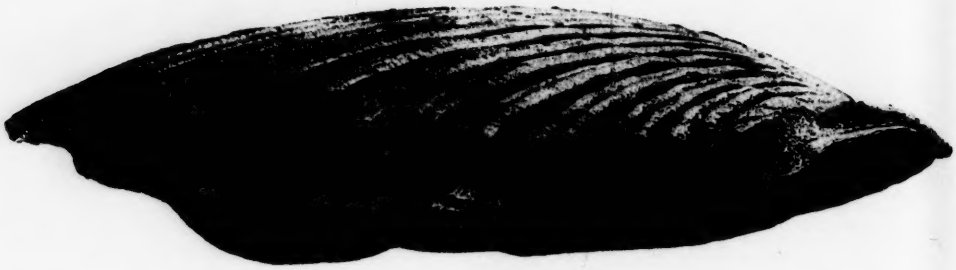

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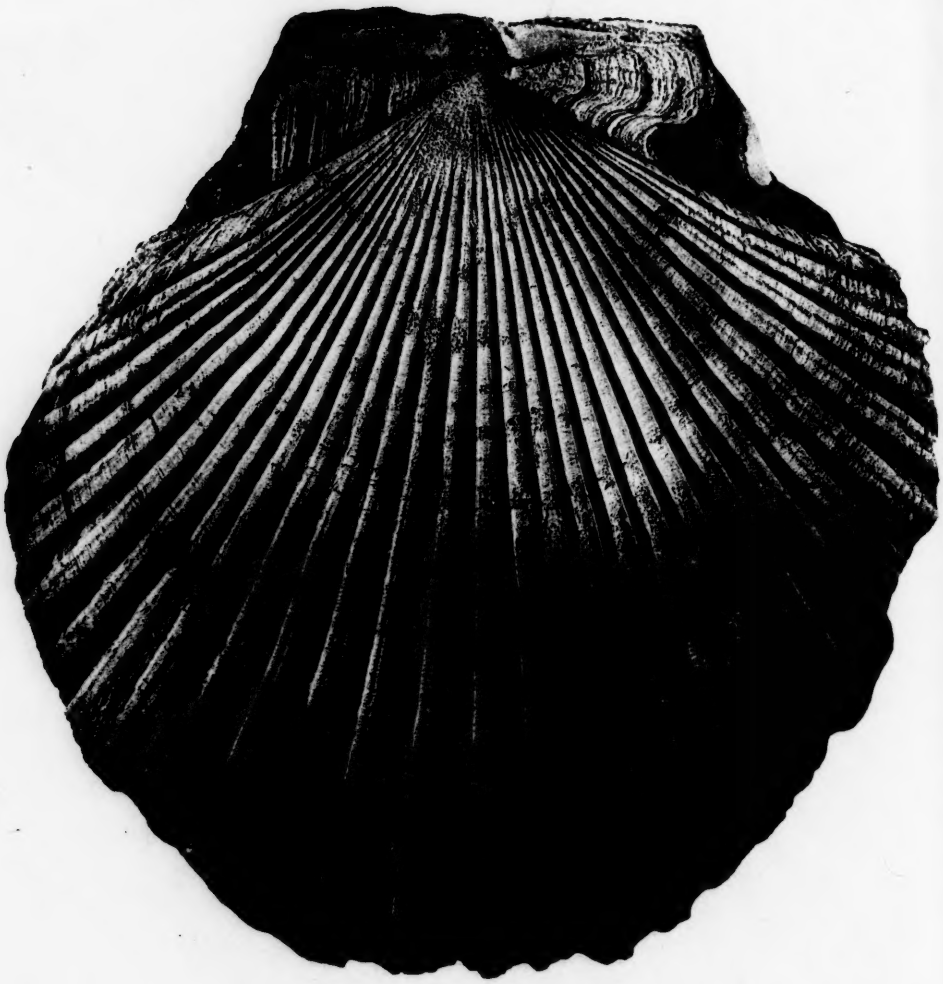

2

TABLE 1—*Continued*

Invertebrates	Status	Reference	Locality	USNM Catalogue Number	Number of Specimens
Cephalopods: Cretaceous: *Ammonites swallowii* Shumard	Holotype? [Specimen smaller than measurements given; may be broken]	Shumard, 1860, p. 591–592	Grayson Co., 4½ miles north of Sherman, and bluffs of Red River, in Fannin and Lamar Cos., Texas	129189	1
Ammonites aculo-carinatus Shumard	Holotype	Shumard, 1853, p. 197, pl. 3, fig. 1	Cross Timbers, Texas	129185	1
Ammonites vespertinus Morton	[Probably specimen discussed by Shumard]	Shumard, 1853, p. 196	Fort Washita. [Northwestern Bryan Co., Okla.]	129190	1
Sub-Carboniferous [Mississippian]: *Goniatites oweni* Hall	Figured specimen	White, 1881, p. 514–515, pl. 7, figs. 3,4	Kinderhook division, Rockford, Indiana	135214	1
Mississippian: *Imiloceras pfefferae* Miller & Werner	Holotype	Miller & Werner, 1942, p. 480–481, text figs. 2A–C	Near base of the Fern Glen limestone, about 1 mile east of Valmeyer, Monroe Co., Illinois	135225	1
Trilobites: Lithographic limestone [Mississippian]: *Proetus missouriensis* Shumard	Figured syntype	Shumard, 1855, p. 196–197, pl. B., figs. 13a,b. [Specimen fig'd pl. B, fig. 13b, missing?]	At Hannibal, Louisiana, and Chouteau Springs, Missouri	135227	1
Archimedes limestone [Mississippian]: *Phillipsia meramecensis* Shumard	——	——	Archimedes limestone, Fenton, St. Louis Co., Missouri	135231, 135232, and 135233	3
Echinoids: Cretaceous: *Holaster simplex* Shumard	Holotype	Shumard, 1853, p. 198–199, pl. 3, fig. 2	Fort Washita. [Northwestern Bryan Co., Okla.]	129186	1
Hemiaster elegans Shumard	Holotype	Shumard, 1853, p. 198, pl. 2, figs. 4a,b,c	Fort Washita. [Northwestern Bryan Co., Okla.]	129187	1
Sub-Carboniferous [Mississippian]: *Lepidesthes colletti* White	Holotype	White, 1878, p. 33–34. [Fig'd by White, 1882, p. 362–363, pl. 41, figs. 2,3; *not* specimen fig'd by White, 1880, p. 163, pl. 40, fig. 2a]	Probably equivalent with the Keokuk division, Salem, Washington Co., Indiana	135221	1

EXPLANATION OF PLATE 116

FIGS. *1,2*—*Patinopecten coosensis* (Shumard). *1*, lectotype, anterior view, showing folded left anterior ear, Empire formation, Pliocene(?), Coos Bay, Oregon, USNM 562472, ×1; *2*, same specimen, right valve, ×1.

TABLE 1—*Continued*

Vertebrates	Status	Reference	Locality	USNM Catalogue Number	Number of Specimens
Perissodactyla:					
Oligocene:					
Palaeotherium(?) proutii Owen, Norwood, & Evans	Figured type [Lower jaw]	Owen, Norwood, & Evans, 1850, p. 66. [Fig'd by Prout, 1846, text fig., and by Leidy, 1852, table 9, fig. 3a. Author of species is not Leidy, oral communication, C. L. Gazin]	Badlands, Chadron [fm.], Nebraska	21820	1
Artiodactyla:					
Oligocene:					
Merycoidodon culbertsoni Leidy	——	——	White River formation, Sioux Co., Nebraska	21819	1

Family NUCULANIDAE

Genus YOLDIA Möller, 1842

Type.—*Yoldia arctica* (Gray) Möller, 1842 = *Y. hyperborea* (Gould).

Subgenus KALAYOLIDA Grant & Gale, 1931

Type.—*Yoldia cooperi* Gabb, 1865

YOLDIA (KALAYOLDIA) OREGONA (Shumard)

Pl. 115, figs. 2,3

Leda oregona Shumard, 1858, p. 121–122 (reprinted in Dall, 1909, p. 187). Gabb, 1869, p. 121.

Nuculana oregona (Shumard). Meek, 1864, p. 5,27. Conrad, 1866, p. 3.

Neilo oregona (Shumard). Conrad, 1865, p. 153.

Yoldia (*Cnesterium*) *oregona* (Shumard). Dall, 1909, p. 105,187, pl. 19, fig. 4.

Yoldia oregona (Shumard). Arnold & Hannibal, 1913, p. 576. Grant & Gale, 1931, p. 130.

Yoldia (*Portlandia*) *oregona* (Shumard). Weaver, 1942 (1943) [in part], p. 49, pl. 9, fig. 16; *not* pl. 9, fig. 8.

Not *Yoldia* (*Cnesterium*) *oregona* (Shumard). Dall, 1922, p. 310.

Not *Yoldia oregona* (Shumard). Etherington, 1931, p. 67, pl. 1, fig. 8.

The single specimen is labeled "*Yoldia oregona* Shumard, Tertiary, Miocene, S. of Oregon City, Ore., Dr. J. Evans, 1851". It is an external impression in a buff, fine-grained, tuffaceous sandstone. This specimen (USNM 562470) is here designated the lectotype of "*Leda*" *oregona* Shumard (pl. 115, fig. 3).

Shumard's original description of "*Leda*" *oregona* reads in part: "The specimens in the collection were obtained by Dr. Evans and the writer, in the autumn of 1851, from the Willamette Valley, a few miles south of Oregon City, Oreg. They are all internal casts in fine-grained, soft, yellowish and white argillaceous sandstone of the Miocene epoch. Their surfaces are coated with a thin film of brown hydrated oxide of iron." Dr. Evans arrived in Oregon City late in September or early October (E. F. Lange, written communication). The iron stain described by Shumard is present on the lectotype, which is 39.5 mm. long (broken at posterior end) and 20.8 mm. high (umbo broken). Shumard gave the length as 20 lines and the height as 10 lines—42.2 mm. and 21.2 mm. respectively. The lectotype agrees with Shumard's measurements and with the original description of the species and matrix.

The lectotype of *Yoldia* (*Kalayoldia*) *oregona* is of moderate size, slightly inflated, and the impression shows faint traces of concentric lines. The umbos are slightly anterior to the middle of the shell. The anterior end is evenly rounded; the posterior end is attenuated and recurved. The posterior hinge line is concave and consists of about 20 teeth; the anterior hinge line, which is convex, of about 25 teeth.

A broken, distorted, cast of the interior of a double-valved specimen (USNM 562471) is considered a paratype? of *Yoldia* (*Kalayoldia*) *oregona*, although labeled *Leda willamettensis* (pl. 115, fig. 2).

Dall (1909, p. 105, pl. 19, fig. 4) described and illustrated a sandstone mold of the exterior of a left valve of *Y.* (*K.*) *oregona*

(USNM 110450) collected by A. J. Collier at Halls Ferry, 6 miles southwest of Salem, Marion County, Oregon. Dall's specimen appears to be conspecific with *Y.* (*K.*) *oregona*, but is larger than the lectotype (47.7 mm. long and 24.9 mm. high) and shows strong concentric lines. A broken cast of the interior of a left valve in Dall's lot (USNM 110449), which was not figured, shows about 19 teeth on the posterior hinge.

Yoldia (*Kalayoldia*) *oregona* has been recorded from the Oligocene of Oregon and the Miocene of Oregon, Washington, and Vancouver Island. The specimen figured by Etherington (1931, p. 67, pl. 1, fig. 8), from the Astoria formation, of Miocene age, in southwestern Washington, appears to be closely related to specimens of *Yoldia temblorensis* Anderson and Martin in the collections at the National Museum from the Temblor formation, of middle Miocene age, in California. The specimens from Reagan's early Pliocene Quillayute formation in Washington, described by Reagan (1909, p. 206, pl. 4, fig. 34) as *Yoldia cooperi* Gabb and later assigned by Dall (1922, p. 310) to *Yoldia* (*Cnesterium*) *oregona*, are not *Y.* (*K.*) *oregona*. Reagan's specimens are poorly preserved, but appear to be closely related to *Y. cooperi*. There are no specimens from the Miocene of Oregon or Washington in the Museum's collections that can be positively identified as *Yoldia* (*Kalayoldia*) *oregona*. *Y.* (*K.*) *oregona* is probably restricted to the Oligocene.

Family PECTINIDAE

Genus PATINOPECTEN Dall, 1898

Type.—Pecten caurinus Gould.

PATINOPECTEN COOSENSIS (Shumard)

Pl. 115, figs. 1,4; pl. 116, figs 1,2; Pl. 117, fig. 4.

Pecten coosensis Shumard, 1858, p. 122 (reprinted in Dall, 1909, p. 187). Gabb, 1869, p. 122. Arnold & Hannibal, 1913, p. 590. Howe, 1922, check list opposite p. 92.

Pecten (*Patinopecten*) *coosensis* Shumard. Dall, 1898, p. 700, pl. 26, fig. 2. Arnold, 1906, p. 61–62, pl. 6, fig. 2; pl. 7, figs. 2,2a. Dall, 1909, p. 112,187, pl. 16, figs. 2,2a; pl. 17, fig. 3. Grant & Gale, 1931, p. 193. Weaver, 1942 (1943), p. 92, pl. 18, fig. 1,2; pl. 21, fig. 2,5.

Three specimens are in the original type lot of "*Pecten*" *coosensis* Shumard and are labeled "*Patinopecten coosensis*, Tertiary, Miocene, Empire formation, Coos Bay, Oregon," but not in Shumard's handwriting. The largest and most perfectly preserved of the three specimens (USNM 562472) is designated the lectotype (pl. 116, figs. 1,2). The lectotype is more than 125 mm. high (broken at ventral margin) and more than 133 mm. in maximum width (broken at anterior and posterior margins).

The right valve of the lectotype (pl. 116, figs. 1,2) is moderately inflated and bears 27 flat-topped, undercut, flanged ribs. The ribs are irregularly grooved near the ventral margin, and the first anterior and first posterior ribs are split. The interspaces are slightly narrower than the ribs or of the same width, and are evenly rounded. The right anterior ear has a deep byssal sinus and is sculptured with 3 riblets; the right posterior ear is truncated at right angles to the hinge and has faint riblets that disappear before reaching the posterior margin.

The left valve of the lectotype is not completely exposed, but it has at least 23 ribs, sharply rounded at the anterior and posterior margins and slightly flattened on the remaining shell. The interspaces are slightly wider than the ribs and are evenly rounded. The left anterior ear has a deep fold at the dorsal margin and is sculptured with faint riblets; the left posterior ear is not exposed.

The smallest paratype (USNM 562473) is incomplete, parts of both valves are missing. The right valve has more than 25 ribs (probably 27), which are flat-topped and smooth, having no grooves or splitting, and are undercut; the interspaces are as wide as the ribs or slightly wider, and are rounded. The left valve is incomplete but had more than 21 ribs, which are slightly flattened near the middle of the shell and sharply rounded on the remainder of the shell.

The largest paratype (USNM 562473) is incomplete: both the right and left valves are broken at the ventral margins and the ears are missing. The right valve bears 28 flat-topped, slightly undercut ribs, none of them grooved except the first anterior and

posterior ribs, which are medially split. The interspaces are as wide as the ribs or slightly wider, and are evenly rounded. The left valve has 27 narrow sharply rounded ribs, with interspaces that are slightly wider to almost twice as wide. There are Recent barnacles attached to the left valve of this specimen, which indicates that the specimen may have been collected from the Empire formation where it is exposed to tide, as it is at Fossil Point, Coos Bay, Oregon.

There are 6 specimens in Dall's (1909, p. 112) lot of *Pecten* (*Patinopecten*) *coosensis* (USNM 107791). The smallest specimen is an incomplete right valve 43.9 mm. high and 44.5 mm. wide (pl. 115, fig. 1). On this specimen there are 25 smooth ribs, which are rounded at the anterior and posterior margins but flat-topped and undercut on the rest of the shell. The right anterior ear has a deep sinus, above which there are perhaps more than 3 riblets (broken at dorsal margin); the right posterior ear does not appear to have riblets.

Three additional specimens in Dall's lot (USNM 107791) were originally more than 111–120 mm. wide and more than 102–113 mm. high. There are 29 to 30 undercut, flat-topped ribs on the right valves (pl. 115, fig. 4), possibly split or irregularly grooved at the anterior margin; the interspaces are rounded; some are as wide as the ribs and some are narrower. The 28 ribs on the left valves (pl. 117, fig. 4) are narrow and steeply rounded at the anterior and posterior margins but may be wider and flat-topped near the middle of the shell. The right anterior ears have a deep byssal sinus, above which there are 3 riblets. The right posterior ears have 4 faint riblets that disappear before reaching the posterior margin. Four to 5 faint riblets are visible on the left anterior ears, which have a deep fold at the dorsal margin. The left posterior ears are truncated at right angles to the hinge and bear 4 faint riblets.

Patinopecten coosensis differs from *Patinopecten propatulus* (Conrad) (1849, p. 726, pl. 18, figs. 13,13a), Astoria formation, Oregon, in having a larger number of ribs on the right valve, and the ribs are narrower, higher, and more undercut and therefore T-shaped than on *P. propatulus*. *P. coosensis* is closely related to *Patinopecten dilleri* (Dal) (1901, p. 117–118), which has been found in the Pliocene of California and Baja California.

P. coosensis has been found in the Empire formation, of Pliocene(?) age, in Oregon and in Weaver's (1912) Miocene Montesano formation in Washington. *P. coosensis* has been questionably identified by Jordan & Hertlein (1926, p. 417) as occurring in the Pliocene of Mesa del Elefante, Laguna Ojo de Liebre (Scammon Lagoon), Baja, California.

"LUCINA FIBROSA" Shumard, nomen dubium

Lucina fibrosa Shumard, 1858, p. 120 (reprinted in Dall, 1909, p. 186).

According to Shumard (p. 120) this species was collected from " . . . dark argillaceous shale at Port Orford, Oregon Territory, and at Davis' Coal Mine." Shumard's "dark argillaceous shale at Port Orford . . . " may be part of the Arago group, of Eocene age. The Arago is exposed in the Port Orford area and is described (Wells, 1955), in part, as "in places gray to black rhythmically bedded shales quite carbonaceous in some places and locally containing beds of coal . . . " The location of the Davis coal mine is not given in Shumard's report, and no record of such a mine in the Port Orford area has been found. It is possible that this mine was located in the Davis Slough coals at Coos Bay, Oregon. Allen and Baldwin (1944, p. 137) say, in describing the Davis Slough coals, "Coaly material shows in a small stream which enters a large tributary of Davis Slough in the NW¼ SE¼ sec. 21, T. 26 S., R. 13 W. A small dump nearby indicated some prospecting, although no opening could be detected." The "Isthmus Slough mine" was opened by A. J. Davis in 1856. Dr. Evans visited mines in the Coos Bay and Port Orford areas in 1856. It is possible that Dr. Evans was not in these areas in 1851 (Written communication, E. F. Lange).

"*Lucina fibrosa*" is probably not a lucinid, if Shumard's description is to be taken literally, so the generic assignment is uncertain. The type specimen has not been

found, and the original description was brief and not accompanied by an illustration. "*Lucina fibrosa*" is therefore to be considered a *nomen dubium*.

Family VENERIDAE
Subfamily CHIONINAE

Genus CHIONE Megerle von Mühlfeld, 1811

Type.—*Chione dysera* Megerle von Mühlfeld = *Venus cancellata* Linné.

Subgenus SECURELLA Parker, 1949

Type.—*Venus securis* Shumard.

Securella is so closely related to *Chione, s. s.*, that it has been assigned subgeneric rank (Keen, 1951, p. 6) although *Securella* was originally proposed by Parker (1949, p. 587) as a generic name. *Securella* is a northern extinct subgenus. It differs from *Chionopsis* Olsson, 1932, (p. 111–112), a southern Miocene to Recent subgenus, in outline and ornamentation. *Chionopsis* is more produced anteriorly and more obliquely truncated posteriorly than *Securella*, and in addition to concentric lamellae has strong radial ribs on the exterior of the shell. (*Gnidiella* Parker, 1949, p. 582, is a synonym of *Chionopsis*.)

CHIONE (SECURELLA) SECURIS (Shumard)
Pl. 117, figs. 1–3.

Venus securis Shumard, 1858, p. 122 (reprinted in Dall, 1909, p. 187–188). Arnold & Hannibal, 1913, p. 590.
Chione securis (Shumard). Dall, 1909, p. 120, pl. 11, fig. 8; pl. 13, figs. 2,8,9. Arnold, 1909, pl. 15, fig. 2. Martin, 1916, p. 251. Clark, 1929, pl. 43, figs. 2,4. Weaver, 1942(1943), p. 162–164, pl. 36, figs. 8,9,13; pl. 37, fig. 8; *not* pl. 39, fig. 15.
Venus parapodema Dall, 1909, p. 122, pl. 11, fig. 11; pl. 13, fig. 1.
Chione aff. *securis* (Shumard). Etherington, 1931, p. 80–81, pl. 8, fig. 5; *not?* pl. 7, fig. 4.
Venus (*Chione*) *securis* Shumard. Grant & Gale, 1931, p. 320, pl. 17, fig. 1.
Securella securis (Shumard). Parker, 1949, p. 587,593, pl. 94, figs. 8,12,19; pl. 95, fig. 6.

This species is the type of *Securella*. Ten specimens in the original type lot of "*Venus*" *securis* are labeled "*Venus securis* Evans and Shum., Miocene Tertiary, Oregon." The label is old and on it is printed, "Shumard Cabinet, Bonham's Seminary," but it has not been possible to determine if the handwriting on the label is Shumard's. One of the specimens is not a *Chione*, and I would identify it as *Spisula?* sp. (USNM 562476). One of the largest and best-preserved specimens of "*V.*" *securis* in the type lot is double-valved and has a small paper label glued to the left valve on which is written "*Venus securis* Shum.," in the same handwriting as that on the label for the entire lot. This specimen is designated the lectotype (pl. 117, figs. 1,3, USNM 562474).

The lectotype is 77.3 mm. long, 69.8 mm. high, and 42.3 mm. wide (both valves). Both valves are worn: the outer shell layers are missing, and the internal radial ribs are exposed. Patches of the outer shell are preserved on some of the paratypes (USNM 562475), and these show concentric lamellae masking the radial ribs.

Chione (*Securella*) *securis* is a moderately large species with irregularly spaced concentric ridges that seem to have been produced to form lamellae. Beneath the concentric ridges there are strong, closely-spaced radial ribs; on worn specimens only the radial ribs can be seen. The lunule is impressed and of moderate size, and the escutcheon is long and deeply impressed. The anterior margin is evenly rounded, and the posterior margin is angulated and abruptly terminated at the ventral margin. The right posterior cardinal is heavy and straight and parallels the ligament pit. The right anterior cardinal is split; the posterior part is slightly curved towards the anterior margin and the anterior part is smaller and more recurved anteriorly (pl. 117, fig. 2).

Shumard in the original locality description of "*V.*" *securis* stated that the specimens were collected " . . . at the mouth of Coose Bay, Cape Blanco, and on the shores of the Columbia a short distance above Astoria, Oreg." None of the 9 specimens in the original type lot resembles the Miocene species *Chione* (*Securella*) *ensifera* (Dall) in the collections at hand from the Astoria formation of Oregon. They all closely resemble specimens of "*V.*" *securis* collected by Camman from "Empire beds, Coos Bay, Oregon" and described and illustrated by Dall (1909, p. 120, pl. 11, fig. 8; pl. 13, figs,

2,8,9). The type lot may have been collected from the Empire formation at the mouth of Coos Bay or Cape Blanco, Oregon. It seems more probable that the specimens were collected at Coos Bay, and the type locality is here so restricted.

"Venus" parapodema Dall (1909, p. 122, pl. 11, fig. 11; pl. 13, fig. 1) is conspecific with *"V." securis* Shumard. The two specimens in Dall's type lot and 4 other specimens labeled by Dall are smaller than any of the specimens of *"V." securis* in the collections at the Museum, and are sufficiently well preserved to have retained the concentric lamellae. A small patch of the radial ribs is visible on a single worn spot on a left valve. Although the hinge is not exposed on either of the specimens in Dall's type lot, *"V." parapodema* has the outline and ornamentation of *"V." securis*.

Chione (*Securella*) *securis* may be distinguished from *Chione* (*Securella*) *ensifera* (Dall) (1909, p. 122–123), Astoria formation (Miocene) of Washington and Oregon, by its larger size, higher beaks, stronger radial ornamentation, and posterior angulation.

Chione (*Securella*) *securis* has been collected in southwestern Washington from Weaver's Montesano formation (Miocene); in Oregon from the Empire formation (Pliocene?); and in California from the Wildcat formation of Lawson, 1894, (Pliocene) of Humboldt Co., and the Etchegoin formation (Pliocene) of Fresno Co.

"CORBULA EVANSANA" Shumard, nomen dubium

Corbula evansana Shumard, 1858, p. 120–121 (reprinted in Dall, 1909, p. 186–187).

This species as described by Shumard is a *Corbula* and may be closely related to *Corbula hornii* Gabb, which has been found at Cape Arago, Coos Bay, Oregon, and at other places in the Coast Ranges of California, Oregon, and Washington.

According to Shumard (p. 121), "This species is exceedingly abundant in the dark aluminous shale at Davis' Coal Mine, and at the Coal Mines of Port Orford . . ." The Davis coal mine is discussed above under *"Lucina fibrosa."* Shumard's "Coal Mines of Port Orford" might be in the coal exposed in the Eckley area (Mason & Erwin, 1955, p. 4, pl. 1); this coal occurs in the Arago group, of Eocene age.

"Corbula evansana" is considered a *nomen dubium*, for the type specimen has not been found and the original description was not accompanied by an illustration.

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EXPLANATION OF PLATE 117

FIGS. *1–3*—*Chione* (*Securella*) *securis* (Shumard). *1*, lectotype, right valve, showing radial ribs, restricted type locality, Empire formation, Pliocene(?), Coos Bay, Oregon, USNM 562474, ×1; *2*, hinge of right valve (Figured by Dall, 1909, pl. 11, fig. 8.), Empire formation, Pliocene(?), Coos Bay, Oregon, USNM 153971, ×1½; *3*, lectotype, dorsal view, showing escutcheon and lunule, USNM 562474, ×1.

4—*Patinopecten coosensis* (Shumard), left valve (Figured by Arnold, 1906, pl. 6, fig. 2; and by Dall, 1909, pl. 17, fig. 3), Empire formation, Pliocene(?), Coos Bay, Oregon, USNM 107791, ×1.

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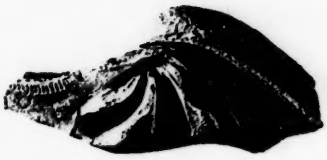

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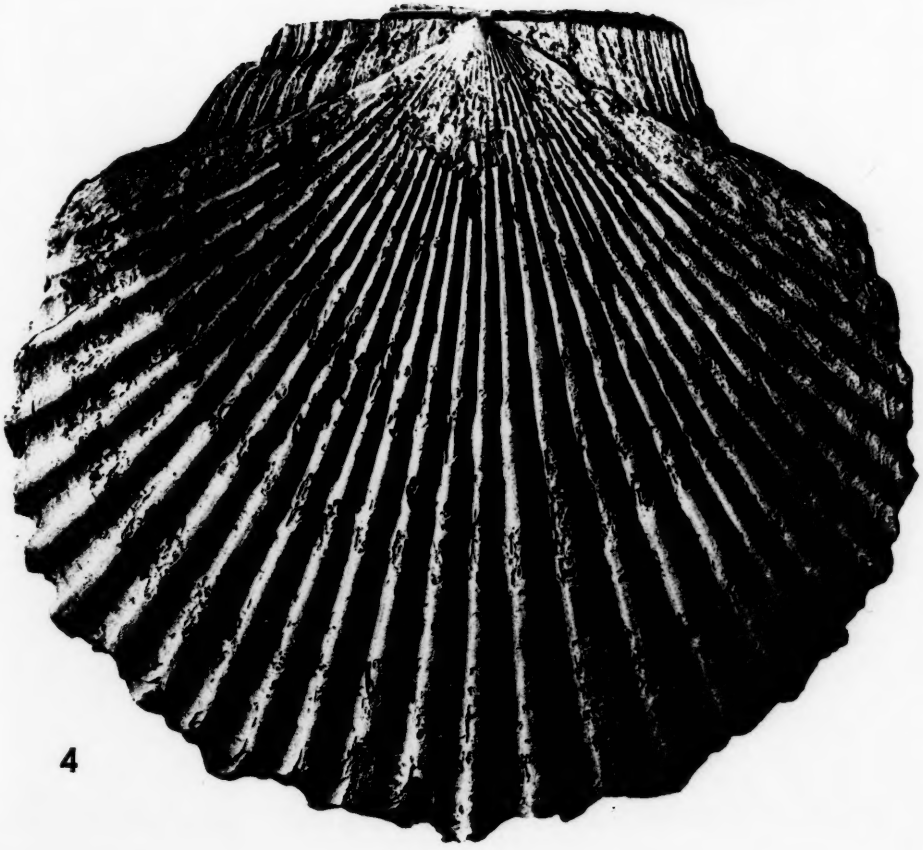

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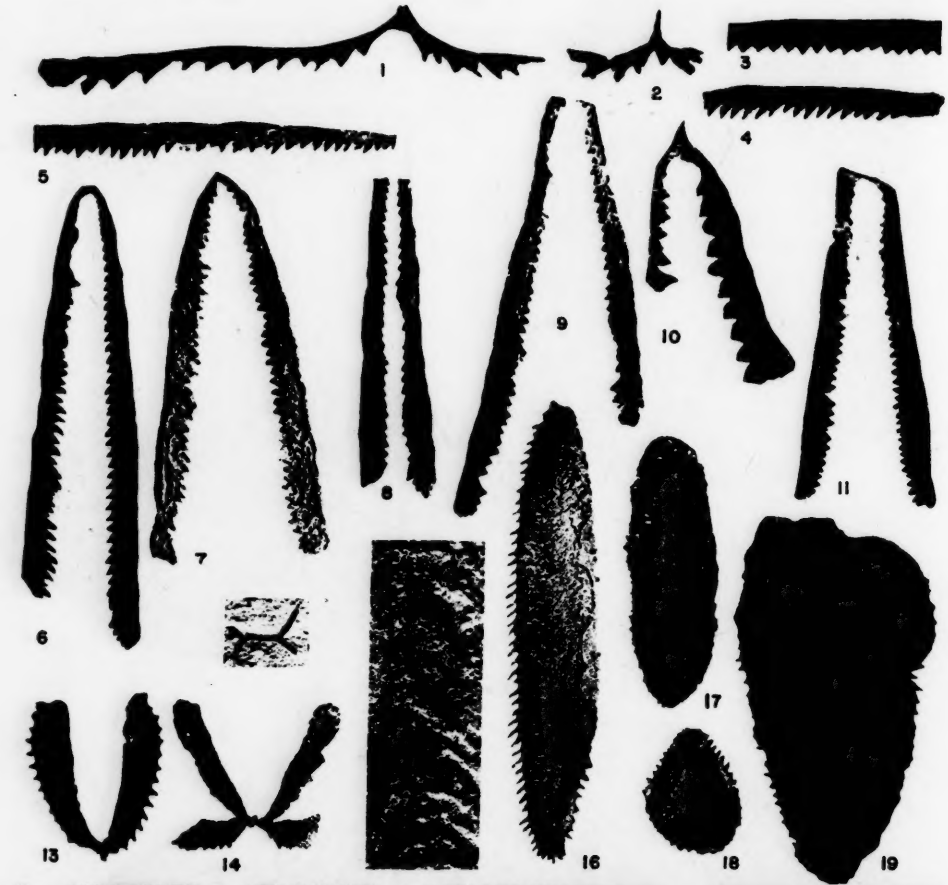
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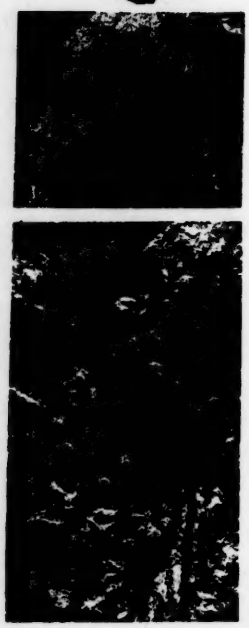
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JOURNAL OF PALEONTOLOGY, V. 32, NO. 5, P. 907–917, PL. 118, 1 TEXT-FIG, SEPTEMBER 1958

LOWER ORDOVICIAN GRAPTOLITE FAUNAS OF WESTERN UTAH

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ABSTRACT—The new species *Desmograptus? utahensis*, and the new varieties, *Phyllograptus ilicifolius* var. *stansburyensis*, and *Phyllograptus angustifolius*, var. *pogonipensis* are described. In addition various species of *Phyllograptus*, *Tetragraptus*, *Didymograptus*, and *Dictyonema* are figured and described from western Utah specimens. A tentative graptolite zonation, tied to trilobite zones already established, is presented, based on the stratigraphic distribution of 16 species.

INTRODUCTION

ONLY scattered graptolite faunas have been reported from Utah, and most of these are either faunal lists or descriptions of single specimens. White (1877) described *Phyllograptus loringi* from the Fish Spring Range in western Utah. Later, Clark (1935) described the occurrence of *Clonograptus flexilis* (Hall), *Didymograptus* cf. *D. bifidus* (Hall), *Dictyonema rectili neatum* Ruedemann. *Desmograptus intricatus* Ruedeman, and *Dictyonema* sp. from the Garden City limestone and *Didymograptus nitidus* (Hall) and *Didymograptus bifidus* (Hall) from the Swan Peak quartzite in the Logan area in northeastern Utah. In 1947 Ruedemann, in a monograph of the graptolites of North America, pointed out the occurrence of

EXPLANATION OF PLATE 118

All specimens ×2 unless otherwise stated

FIGS. *1,2,4,5—Didymograptus patulus* (Hall). *1,2*, carbon film of initial portion of rhabdosome ×4; *4,5*, carbon films of portions of distal ends of stipes. All specimens from Swan Peak quartzite, southern Stansbury Mountains, B.Y.U. locality 10001.

3—Didymograptus nitidus (Hall). Carbon film of distal portion of stipe from Swan Peak quartzite, southern Stansbury Range, B.Y.U. locality 10001.

6,7—Didymograptus artus Elles and Wood. Nearly complete rhabdosomes from lower Garden City limestone, northern Stansbury Range, B.Y.U. locality 10951.

8,9,11—Didymograptus bifidus (Hall). *8,9*, partially pyritized specimens from Kanosh shale, Simpson Range, B.Y.U. locality 10953; *11*, carbon film from Kanosh shale, Fossil Mountain, southern Confusion Range, B.Y.U. locality 10942.

10—Didymograptus sp. Juvenile portion of rhabdosome ×4.

12—Tetragraptus? quadribranchiatus (Hall). Broken initial portion of rhabdosome from upper Wahwah limestone, southern Confusion Range, B.Y.U. locality 10950.

13,14—Tetragraptus similis (Hall). Well preserved carbon films of nearly complete rhabdosomes from upper Wahwah limestone, southern Confusion Range, B.Y.U. locality 10950.

15,16—Phyllograptus angustifolius Hall var. *pogonipensis* Rigby, n. var. *15*, portion of holotype stipe showing prominent apertural mucros; ×4; *16*, holotype impression in partially metamorphosed shale from lower Garden City limestone, northern Stansbury Mountains, B.Y.U. locality 10951.

17—Phyllograptus ilicifolius Hall var. *stansburyensis* Rigby, n. var. Holotype specimen from lower Garden City limestone, northern Stansbury Range, B.Y.U. locality 10951.

18—Phyllograptus anna Hall. Carbon film and impression from upper Wawah limestone, southern Confusion Range, B.Y.U. locality 10950.

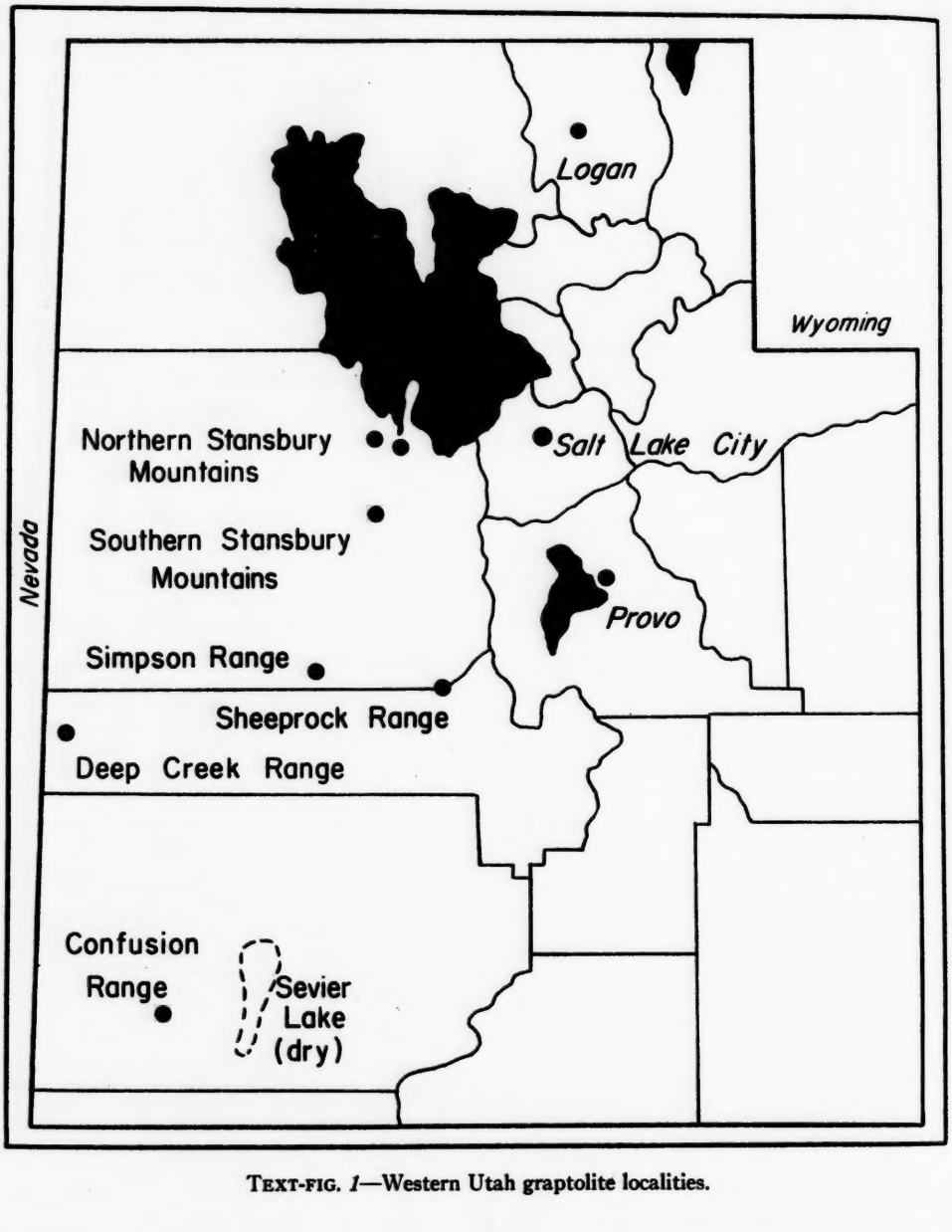
19—Phyllograptus ilicifolius var. *grandis* Elles. Nearly complete specimen collected from Chokecherry dolomite in Deep Creek Range.

20—Dictyonema sp. cf. *D. filiramus* Gurley. A single poorly preserved impression of part of rhabdosome from Garden City limestone, southern Stansbury Range, B.Y.U. locality 10940, ×1.

21—Desmograptus(?) utahensis Rigby n. sp. Holotype from lower Garden City limestone, northern Stansbury Mountains, B.Y.U. locality 10949.

22—Dictyonema merriami Ruedemann. Small portion of rhabdosome from Fillmore limestone, southern Confusion Range, sample 12, Section G, Hintze, 1951. ×2.5.

Didymograptus patulus (Hall) and *Didymograptus nitidus* (Hall) on Grantsville Peak in the Stansbury Range in eastern Tooele County, Utah (fig. 1). Ruedemann (1947, p. 326) also lists *Didymograptus artus* Elles and Wood as occuring in Ogden Canyon, in the Wasatch Mountains east of Ogden, Utah. In 1948 Williams, in a study of the Paleozoic rocks of the Logan quadrangle, published a faunal list of graptolites in the Garden City limestone and Swan Peak quartzite. In addition to the forms reported by Clark, Williams (1948, p. 1136) reports *Tetragraptus* sp. from the Garden City



TEXT-FIG. 1—Western Utah graptolite localities.

limestone. Ross made a systematic study of the Garden City formation (1951) and, although primarily interested in its trilobite faunas, noted the occurrence of various graptolites and tied his collections to measured sections and trilobite zones. Hintze (1951) in a similar study of the Pogonip group in western Utah, adopted Ross' trilobite zones and also noted the presence of various graptolite genera in measured sections in the southern end of the Confusion Range in western Millard County. Croft (1956) reported *Didymograptus murchisoni* (Beck), *D. nitidus* (Hall), and *D. patulus?* (Hall) from the Swan Peak quartzite in the southern end of the Stansbury Range in Tooele County, Utah.

In recent years several new localities have been discovered which yield new forms, as well as additional stratigraphic information.

STRATIGRAPHY

Three formation names have long been used in Utah to denote the lower Ordovician. The term Garden City has been used in northeastern and northern Utah, the term Opohonga has been used in the Tintic mining district of central Utah and surrounding areas, and Pogonip limestone has been used for equivalent rocks in western Utah and eastern Nevada. It is not the purpose of the present paper to discuss problems of the stratigraphy of these formations, but to call attention to the graptolite faunas.

Pogonip Group

Nomenclature of the Pogonip limestone in western Utah and eastern Nevada has differed among investigators. Recently it has been studied in detail by L. F. Hintze (1949, 1951), who elevated it to group rank and erected within it six new formations which were correlated with trilobite zones established by Ross (1949, 1951) in the Garden City limestone of northeastern Utah. The formations of the Pogonip group are, in ascending order: the House limestone, Fillmore limestone, Wahwah limestone, Juab limestone, Kanosh shale, and Lehman formation. Lithologic character and thickness of the formations are summarized below from Hintze (1951, pp. 11–20).

The House limestone consists of medium gray, medium to thin-bedded, cherty, silty calcilutite. It is approximately 475 feet thick at the type locality in the House Range. The overlying Fillmore limestone is a series of interbedded intraformational limestone conglomerate, limy siltstone, muddy limestone and limy shale with occasional thin beds of calcilutite. Intraformational conglomerate is common in the entire Pogonip group, but is especially abundant in the Fillmore limestone. The formation is approximately 1500 feet thick in the type area, and is the thickest formation in the Pogonip group; it thins to the north and east, and is only 700 feet thick in central Utah, but thins to a feather edge in central and eastern Utah County.

The slope-forming Fillmore limestone grades upward abruptly into the overlying ledge-forming, quartzose calcisiltite of the Wahwah limestone. The Wahwah limestone is abundantly fossiliferous and it, or its faunal equivalent, is recognized over most of the Great Basin. The Wahwah is only 227 feet thick in the type area.

Juab limestone crops out on top of the Wahwah limestone and is characterized by medium gray, fine sandy calcisiltite that has a distinctly slabby appearance. It forms five prominent ledges in its outcrop belt in the southern Confusion Range where it is approximately 139 feet thick.

The Kanosh shale occurs above the Juab limestone and is one of the most distinctive datum horizons of the eastern Great Basin. It is composed of distinctively colored olive, gray, or pink fissile shale with interbedded thin bedded, medium gray calcarenite and calcisiltite that is abuntantly fossiliferous. Thin beds of siltstone and fine-grained sandstone are also locally present. It forms a prominent slope and is approximately 500 feet thick in the southern Confusion Range, at its type locality.

The Lehman formation is uppermost of the Pogonip group, and is composed of thin to thick-bedded, fossiliferous, blue-gray, calcilutite with minor interbedded units of sandstone and siltstone. It forms a distinctive ledge above the slope of the Kanosh shale and below the light-colored ledges of

the Swan Peak quartzite. The Lehman formation is approximately 200 feet thick at its type locality in the southern Confusion Range.

Garden City Limestone

The Garden City limestone can be subdivided into two members. The lower of these is composed of interbedded intraformational conglomerate, muddy limestone, calcisiltite and calcilutite. The lower part of the lower member contains white to light-gray chert (Ross, 1951, p. 7), and in other respects appears similar to the House limestone of the Pogonip group. The upper part of the lower member appears lithologically equivalent to the Fillmore limestone of the Pogonip group.

The upper member of the Garden City limestone is homogenous and is composed of dark gray calcilutite and calcisiltite. It is composed of discontinuous thin-bedded to very thin-bedded laminated units with thin partings of mudstone of shale. Stringers and nodules of black chert are common in every outcrop of the formation. Ross (1951, pp. 6–38) discussed the stratigraphy of the unit and presented detailed stratigraphic sections.

Swan Peak Quartzite

The Swan Peak quartzite overlies the Pogonip group and the Garden City limestone in western and northeastern Utah. Fossils have been found only in the northeastern sections where the formation consists of a lower shale unit and an upper more massive quartzitic unit (Ross, 1951, Webb, 1956). Graptolites occur in the lower shale unit which is approximately equivalent to the Kanosh shale to the west.

SYSTEMATIC PALEONTOLOGY

Subphylum STOMOCHORDA
Class GRAPTOLITHINA
Order DENDROIDEA
Family DENDROGRAPTIDAE

DICTYONEMA MERRIAMI Ruedemann
Pl. 118, fig. 22

Dictyonema merriami Ruedemann, 1947, p. 170, pl. 3, figs. 14,15.

Description.—A single fragment of a rhabdosome 6 mm. wide and 27 mm. long, composed of relatively straight branches that bifurcate only once throughout the length of the specimen. Branches approximately .2 mm. wide separated by .40 to .45 mm. Dissepiments average 8 to 10 per centimeter with branches averaging 18 to 20 per centimeter. Dissepiments slightly thinner to only one half as thick as branches, and spaced to form irregular rectangular net, for most dissepiments are roughly at right angles to branches. Thecae and bithecae not observed.

Discussion.—This specimen differs from the type in having a less closely spaced net of dissepiments. In other characteristics, however, the specimen is like the type described by Reudemann.

Occurrence.—The single specimen was collected by L. F. Hintze from the Fillmore formation in the southern end of the Confusion Range, in Millard County, Utah. It occurs in his sample G-12, Section G (1951, p. 50).

DICTYONEMA sp. cf. FILIRAMUS Gurley
Pl. 118, fig. 20

Dictyonema filiramus (Gurley, MS) Bassler, 1909, U. S. Nat. Mus. Bull. 65, p. 34, text-figs. 38–40.

Description.—Specimen consisting of a fragment 21 mm. across and 25 mm. long composed of impression of branches and dissepiment in argillaceous limestone. Branches spaced 15 to 16 per centimeter, approximately 0.25 to 0.35 mm. thick, separated by approximately same distance near base, and by nearly twice distance in outer part of rhabdosome. Dissepiments thin, occurring 10 or 11 per centimeter, rarely 8 or 9 per centimeter near base. Major branches bifurcating irregularly, mainly from a few major branches in pinnate fashion rather than dichotomously, so that one branch may subdivide along one side five or six times per centimeter, but not branch at all along the opposite side. At a radius of 15 mm. from the base, there are only two such major branches with these being separated by 15 to 18 mm. in that distance. Thecae and bithecae not observed. Branches deflect between dissepiments to form roughly hexagonal openings, elongate in the direction of growth. Branching occasionally dichotomous, but most expansion one-sided from a single branch.

Discussion.—There is some question whether this specimen should be included with *Dictyonema filiramus*, for the Utah specimen is from lower Ordovician rocks whereas the type specimens of the species are from Silurian rocks. The method of branching seen in the Utah specimen is also developed in the Silurian form, and measurements of the Utah specimen agree well with those of the type for *D. filiramus*.

Occurrence.—The single specimen was collected by John Teichert from the lower part of the Garden City limestone in the southern Stansbury Mountains (B.Y.U locality 10940). It was probably collected from rocks of trilobite zone G, for graptolites characteristic of zone H occur considerably higher in the same general area.

DICTYONEMA sp. A

Description.—A fragment of rhabdosome approximately 4 mm. square, composed of rapidly bifurcating basal portion of rhabdosome which shows two branches in lower part and five in upper. Branches .3 to .4 mm. across, separated by one-fourth to one-half that distance. Spacing of thick (.3 mm.) dissepiments varies from 1 to 2 mm. in fragment.

Occurrence.—The single fragment occurs in sample G-12 collected by L. F. Hintze (1951, p. 50) from Section G, in the Fillmore limestone, southern Confusion Range in western Millard County, Utah. The specimen is from trilobite zone G of Hintze (1951) and Ross (1951).

DESMOGRAPTUS(?) UTAHENSIS, n. sp.
Pl. 118, fig. 21

Description.—Fragment of dendroid rhabdosome 43 mm. wide and 32 mm. long showing all but earliest portions of colony. Composed of relatively thick branches, .8 mm. across, separated by 2.0 to 3.0 mm. Branches bifurcate approximately every 10 to 12 mm., but some individual branches do not bifurcate throughout their entire length. Anastomoses relatively common but irregular, dissepiments very rare and irregularly spaced. Entire rhabdosome of open anastomosing mesh lacking the regular symmetry of most other species of the genus.

Diagnosis.—*Desmograptus? utahensis* differs from other related forms in its thick branches, irregular anastomoses, and spacing of branches.

Discussion.—*Desmograptus? utahensis* appears as an intermediate form between more characteristic regularly anastomosing desmograptids and *Dictyonema*. It is unfortunate that individual thecae are not preserved which would allow more definite generic assignment.

Occurrence.—The single specimen was collected from float of the Fillmore limestone equivalent in the Garden City limestone at the northern tip of the Stansbury Mountains, in a highway road cut at Tempie, eastern Tooele County, Utah. Locality 10949. Collected by the writer and L. F. Hintze.

Holotype.—Brigham Young University, 10949-1, at Type Collections Repository, Brigham Young University, Provo, Utah.

Order GRAPTOLOIDEA
Family DICHOGRAPTIDAE
Section TETRAGRAPTI
Genus TETRAGRAPTUS
TETRAGRAPTUS SIMILIS (Hall)
Pl. 118, figs. 13,14

Phyllograptus similis Hall, 1858, Geo. Survey Canada, Rept. for 1857, p. 140.
Didymograptus caduceus Salter, 1863, Geol. Soc. London, Quart. Jour., vol. 19, p. 137, fig. 13b.
Graptolithus bigsbyi Hall, 1865, Can. Organic Remains, p. 86, figs. 22–30.
Tetragraptus bryonoides Etheridge, Jr., 1874, Ann. Mag. Nat. Hist., ser. 4, vol. 14, p. 2, pl. 3, figs. 1,2, not figs. 3,4.
Tetragraptus caduceus Brögger, 1882, Sil. Etagen 2 and 3 Krist, p. 38.
Tetragraptus similis Ruedemann, 1904, N. Y. State Mus. Mem. 7, p. 658–662, text-figs. 58–61, p. 642, fig. 48, p. 644, figs. 49,50, pl. 12, figs. 2–10.

Description. — Rhabdosome relatively small, composed of four reclined stipes, which range from 8 to 12 mm. long and from 1.8 to 3.2 mm. wide. Greatest width of stipes from 2 to 3 mm. from distal end. Stipes relatively straight. Thecae 10 to 14 per centimeter, gently ascending and curved outward. Original angle of divergence approximately 30° gradually shifting to approximately 50° in outer parts of the stipe. Thecae expand gradually and evenly to .7 or .8 mm. at aperture and are up to 3.8 mm. long. Aperture marked by a characteristic apertural denticle or mucro limiting slightly

concave margin. First order branches 1.0 to 1.2 mm. long and 0.5 to 0.6 mm. wide. Second order branches 0.6 to 0.7 mm. wide at point of origin.

Diagnosis.—Suboval reclined tetragraptus with 10 to 14 thecae per centimeter whose stipes have characteristic suboval shape and long mucros.

Occurrence.—The only forms collected to date in Utah occur in the upper part of the Wahwah formation, zone J or K, on the southeastern slope of Fossil Mountain in the southern end of the Confusion Range, western Millard County, Utah (B.Y.U. locality 10948).

TETRAGRAPTUS(?) QUADRIBRANCHIATUS (Hall)
Pl. 118, fig. 12

Graptolithus quadribranchiatus Hall, 1858, Geol. Survey Canada Report for 1857, p. 125.
Graptolites (Didymograpsus) quadribranchiatus McCoy, 1874, Geol. Survey Victoria, Prodr. Pal. Victoria, p. 15, pl. 2, fig. 1.
Tetragrapsus crucialis Salter, 1863, Geol. Soc. London, Quart. Jour., vol. 19, p. 137, fig. 8b.
Tetragrapsus quadribranchiatus Nicholson, 1868, Geol. Soc. London, Quart. Jour., vol. 24, p. 131.
Tetragraptus quadribranchiatus Linnarsson, 1879, Sver, Geol. Unders. ser. C., no. 31, p. 5.
(For a more complete synonymy see Ruedeman 1947, p. 307.)

Description.—The specimens at hand consist of three fragments of the initial portion of the rhabdosome plus associated fragmentary stipes. Rhabdosome apparently composed of four pendant to inclined stipes. First order branches 1.0 mm. long forming a 2.0 mm. connection between second order branches. Stipes .2 mm. thick in both first and second order branches. Second order branches diverge at 94 to 96 degrees in two specimens and 100 to 104 degrees in another specimen. Thecae not well defined in carbon film.

Discussion.—Rhabdosomes collected are too fragmentary for anything but provisional identification. Thecae portions of stipes were not collected in association with the sicular initial portion of the colony. Relationship of the first and second order branches and their thickness indicates this species. It is possible, however, that these initial portions may be *Clonograptus flexilis* (Hall), for that species has been reported by Williams (1948) and Ross (1951) from rocks of approximately the same age in northeastern Utah. Until additional, more complete, fossils are found, there will be doubt concerning the identification of these specimens.

Occurrence.—*Tetragraptus(?) quadribranchiatus* (Hall) occurs in the uppermost Wahwah limestone southeast of Fossil Mountain at the southern end of the Confusion Range, western Millard County, Utah. The form occurs immediately below silty shale that bears *Tetragraptus similis* (Hall) and *Phyllograptus anna* Hall. These fossiliferous horizons are separated by less than a total of ten feet stratigraphically (B.Y.U. locality 10950).

TETRAGRAPTUS spp.

In addition to the forms described above, fragments of several species of *Tetragraptus* have been collected from the Wahwah limestone of the Pogonip group, in the southern part of the Confusion Range. The initial portions of rhabdosomes were not associated with these specimens and specific identification has not been attempted. Indeed, some of these specimens may be fragments of *Clonograptus*, a genus that occurs at this approximate level in northeastern Utah.

Genus PHYLLOGRAPTUS
PHYLLOGRAPTUS ANNA Hall
Pl. 118, fig. 18

Phyllograptus anna Hall, 1865, Can. Organic Remains, p. 124, figs. 11–16.
(For more complete snyonymy see Ruedemann, 1947, p. 316.)

Description.—Rhabdosome small, consisting of four scandent stipes, most specimens semioval with greatest width near antisicular end. Specimens collected range from 5.0 to 5.3 mm. wide and 7.8 to 8.3 mm. long. Thecae simple, elongate, in contact throughout length and directed outward with slight curve, becoming nearly straight toward antisicular end where they subparallel axis of rhabdosome. Thecae range from 18 to 20 per centimeter in collected specimens. Utah forms agree in nearly all respects to the type description of Hall.

Occurrence.—*Phyllograptus anna* is com-

mon in thin-bedded, dark-green shale and siltstone in the upper part of the Wahwah limestone near Fossil Mountain at the southern end of the Confusion Range in western Utah, (B.Y.U 10950). It has also been reported from Ordovician rocks in several localities in eastern Nevada. The Utah specimens are from trilobite Zone K of Hintze (1951).

PHYLLOGRAPTUS LORINGI White

Phyllograptus loringi White, 1877, U. S. Geog. Survey W. 100th Meridian, vol. 4, p. 51, pl. 3, figs. 1a,1b, (Preliminary Report, 1874, p. 9).
Phyllograptus loringi Bassler, 1915, U. S. Nat. Mus. Bull. 92, p. 376.

Description.—A single broken, but complete, specimen in which the rhabdosome consists of four elongate oval to elliptical scandent stipes. Specimen at hand measures 29.0 mm. long and 17.0 mm. wide at the widest part, midway in the rhabdosome. Thecae are elongate and thin, slightly curved in dorsal parts of the stipe and strongly to moderately curved outward in the ventral part. Thecae occur 14 per centimeter, and are approximately 7.5 mm. long and 1.2 to 1.4 wide at the aperture. Apertural characteristics obscured by poor preservation of the specimen.

Discussion.—The specimen collected agrees in most respects with the type specimen found in the same general area in Utah. The type specimen is slightly thinner and more elongate than the one recently found, but the thecal count and general shape are sufficiently similar to allow placing the specimen in this species.

Occurrence.—The type specimen was collected in "strata of the age of the Quebec group of Canada; Fish Spring, House Range, Utah." (Ruedemann 1947, p. 319). The northern part of what was then called the House Range is now termed the Fish Spring Range. The additional specimen, here reported, was collected by L. F. Hintze as float in the upper part of the Fillmore limestone at 658 feet in his measured section H (1951, p. 50–56). Additional representatives of the species have been collected by Mr. Kenneth Bick during field work in the Deep Creek Range in western Juab County.

PHYLLOGRAPTUS ILICIFOLIUS var. GRANDIS Elles
Pl. 118, fig. 19

Phyllograptus ilicifolius var. *grandis* Elles, 1898, Quar. Jour. Geol. Soc. London, vol. 54, p. 493.

Description.—Rhabdosome consisting of four elliptical elongate stipes joined to form the characteristic pattern of the genus. The specimen at hand is 25.6 mm. long and 12.3 mm. wide, with a small portion broken away at the end. Thecae are in contact throughout their length and are distinctly curved through at least 45 degrees in the medial portion of the stipe. Thecae occur 12 to 13 per centimeter and range up to 8 mm. long and 1.0 to 1.2 mm. wide at the aperture. Apertural margin distinctly convex with a pronounced slender elongate mucro up to 0.8 mm. long.

Discussion.—Thecal count, mucrate aperture, overall shape and size of the specimen at hand seem distinctive of this variety of *Phyllograptus ilicifolius*. Ruedemann (1947, p. 319) pointed out the affinity of this variety with *Phyllograptus loringi* White and *Phyllograptus ilicifolius* var. *major*, and seemed reluctant to extend this variety into western North America beyond the Deepskill section in New York state. The striking similarity of the Utah form to the one illustrated by Elles (1898, p. 493) seems conclusive.

Occurrence.—*Phyllograptus iliciformis.* var. *grandis* Elles occurs in the Chokecherry dolomite in the northern part of the Deep Creek Range in western Juab County, Utah. The single specimen was collected by Kenneth Bick.

PHYLLOGRAPTUS ILICIFOLIUS Hall var. STANSBURYENSIS n. var.
Pl. 118, fig. 17

Diagnosis.—This particular variety of *Phyllograptus ilicifolius* is characterized by its size, overall shape, thecal count (18 to 20 er centimeter), and short mucros at the apertural margin.

Description.—Rhabdosome semi-elliptical to elongate elliptical with types being 14 to 15 mm. long and 4.6 to 5.5 mm. wide, composed of four scandent stipes. Thecae 18 to 20 per centimeter, diverge from axis at approximately 45 degrees, varying between

42 and 46 degrees, and curve outward. In lower part of stipe thecae curve so that apertueral portions are at right angles to axis of stipe, but upper portions of thecae are less markedly curved and diverge from axis less than 60 degrees in the apertural portions. Apertures slightly concave with weak to moderate mucros. Thecae range up to 4 mm. long and 0.5 to 0.6 mm. wide at the apertures.

Discussion.—Phyllograptus ilicifolius var. *stansburyensis* differs from other related varieties in its high thecal count and large size. It differs from *P. typus* in thecal count and character of the apertures, as well as size and shape of the rhabdosome. It is differentiated from *P. loringi* on the rhabdosome shape and curvature of the thecae.

Occurrence.—Many complete specimens were collected by the writer and L. F. Hintze from the Garden City limestone, trilobite zone H, from the northern end of the Stansbury Mountains, (B.Y.U. localities 10951, 10952).

Disposition of types.—Type specimens are in the repository of the Geology Department, Brigham Young University Specimen no. 10952-1 is designated as the holotype, and 10952-2 to 15 as paratypes.

PHYLLOGRAPTUS ANGUSTIFOLIUS Hall var. POGONIPENSIS, n. var.
Pl. 118, figs. 15,16

Diagnosis.—Elongate phyllograptid with semielliptic branches and a thecal count of 14 to 15 per centimeter, in which thecae diverge from axis at approximately 45 degrees throughout length of stipe, and in which long mucros develop at the concave aperture.

Description. — Rhabdosome elongate, semielliptic branches of nearly equal width throughout length except in ends where tapering. Tapering is most rapid in sicular end and least rapid, but more pronounced, in antisicular end. Specimens range from 18 to 33 mm. long and from 3.8 to 6.2 mm. wide, with the holotype being 33 mm. long and 6.2 mm. wide. Thecae vary from 14 to 15 per centimeter in the holotype, in other specimens, in various portions of the stipes, 15 per centimeter is the most common. Thecae directed upward and relatively straight, angle of divergence is approximately 45 to 50 degrees with outer portions of thecae curving to approximately 60 or 65 degrees from the axis of the stipe. The angle remains nearly constant throughout the length of the stipes. Thecae are approximately 4.0 mm. long at the widest part of the stipe and 0.6 to 0.7 mm. wide at the aperture. Apertures markedly concave with a pronounced downward deflected mucro at the margin giving a superficial impression of pronounced curving of the thecae in their outer portions. Mucros range from 0.4 to 0.8 mm. long.

Discussion.—This variety of *P. angustifolius* is differentiated from other related forms because of the high thecal count and large size of the specimens. Long mucros at the apertures and the overall shape of the rhabdosome are characteristic of the species and differentiate it from other phyllograptids.

Occurrence.—Many moderately well preserved specimens have been collected from the Garden City limestone, trilobite zone H, in rocks equivalent to the middle part of the Fillmore limestone of the Pogonip group. Specimens have been collected near Flux, and near Tempie, in the northern part of the Stansbury Mountains, and in the southern part of the same range, approximately 3 miles northwest of Johnsons Pass, (B.Y.U. localities 10951, 10952, and 10940). L. F. Hintze and the writer collected the forms at the northern end of the range and John Teichurt collected less well preserved specimens at the southern locality. This variety, in association with *P. iliciformis* var. *stansburyensis* and *P. anna*, seems characteristic of trilobite zone H of the Garden City and Pogonip limestones.

Disposition of types.—Holotype and paratypes are in the repository of the Geology Department, Brigham Young University. Specimen numbers 10952-1 holotype; and 10952-2 to 14, 10951-1, and 19040-1 paratypes.

Section DIDYMOGRAPTI
Genus DIDYMOGRAPTUS
DIDYMOGRAPTUS ARTUS Elles & Wood
Pl. 118, figs. 6,7

Didymograptus artus Elles & Wood, 1901–1918, Mon. Brit. Grapt., Pal. Soc., p. 48, figs. 6a–d.

(For more complete synonymy see Ruedemann, 1947, p. 326.)

Description.—Pendant didymograptid in which stipes are subparallel to mildly diverging composed of thecae which are simple, slightly curved to straight, occurring 17 to 19 per centimeter in the specimens at hand. Thecae diverge from axis at approximately 43 to 50 degrees, and overlap up to two-thirds their length. Thecae approximately 2.0 mm. long and 0.4 mm. wide at the aperture in the distal end of stipe which is up to 31 mm. long and 2.9 mm. wide. Sicula approximately 1.3 mm. long, relatively narrow.

Discussion.—*D. artus* is closely related to *D. bifidus* but can be differentiated from the later by a closer crowding of thecae, and greater angle of divergence of the thecae in the former.

Occurrence.—*Didymograptus artus* occurs in Utah collection in the middle and upper part of the Pogonip group. It occurs in the upper Fillmore limestone in the northern Stansbury Range, (B.Y.U. 10951, 10952) in beds equivalent to the Kanosh shale in the Simpson Range (B.Y.U. 10953) and Sheeprock Range in central Utah. It has also been reported from Ogden Canyon (Ruedemann 1947, p. 326) in central Utah.

DIDYMOGRAPTUS BIFIDUS (Hall)
Pl. 118, figs. 8,9,11

Graptolithus bifidus Hall, 1865, Can. Organic Remains, p. 75, pl. 1, figs. 16–18, pl. 3, figs. 9,10.
Didymograptus bifidus Wood, 1906, Geol. Soc. London Quart. Jour., vol. 62, p. 431–432.
(For additional synonymy to 1906 see Bassler, 1915, U. S. Nat. Mus. Bull. 92 and to 1936 see Ruedemann, 1947, p. 327.)

Description.—Pendant didymograptids in which thecae occur 14 to 16 per centimeter. Thecae straight with overlap of two-thirds to one-half their length. Stipes up to 35 mm. long and 2.4 mm. wide, but average 1.9 mm. wide. Sicula approximately 2.0 mm. long in most specimens at hand, but varies from 1.7 to 2.4 mm. long. Thecae inclined at angles from 38 to 46 degrees. Specimens from Kanosh shale at Fossil Mountain are carbon films but those from the Simpson Range preserved as pyrite models.

Discussion.—Most specimens at hand range slightly higher in thecal counts than the typical specimens which ranged from 13 to 15 per centimeter. In specimens collected from the Kanosh shale, 15 or 16 thecae per centimeter are most common. In other respects, however, Utah specimens fit well the type description.

Didymograptus bifidus and *D. artus* are closely related, often occuring in the same slabs, and may be confused where these species grade into each other in terms of thecal count.

Occurrence.—*Didymograptus bifidus* occurs in profusion in upper green-gray, silty, platy shale of the Kanosh shale at Fossil Mountain in the Confusion Range (B.Y.U. locality 10941). The species also occurs in slightly metamorphosed shale of the Kanosh shale in the Simpson Range. It has also been reported from the Swan Peak quartzite in northeastern Utah (Clark, 1935, pp. 240–241).

DIDYMOGRAPTUS NANUS Lapworth

Didymograptus geminus Nicholson, 1868, Geol. Soc. London, Quart. Jour., vol. 34, p. 134, pl. 5, figs. 8,9.
Didymograptus indentus var. *nanus* Lapworth, 1875, Geol. Soc. London, Quart. Jour., vol. 31, p. 647, pl. 33, fig. 7d; pl. 35, figs. 4a–c.
Didymograptus nanus Elles & Wood, 1901, Mon. Brit. Grapt., pt. 1, vol. for 1901, p. 47, pl. 4, figs. 5a–h.

Description.—A single fragment of a stipe occurs in collections from Utah. This specimen is 8.2 mm. long and 0.8 mm. wide, containing 6 complete thecae and an additional partial one, giving approximately 8 thecae per centimeter. Thecae diverge from stipe at approximately 30 degrees and are relatively straight or gently curved outward. Apertural margin is straight and approximately at right angles to dorsal side of stipe, or approximately 60 degrees to axis of thecae. Thecae approximately 1.8 mm. long and 0.5 to 0.6 mm. wide at the aperture.

Occurrence.—The single specimen known from the state is from the upper part of the Fillmore limestone from the Hackethorn Hills at the southern end of the Confusion Range. Specimen collected by L. F. Hintze (1951) in his Section G, sample 12.

DIDYMOGRAPTUS NITIDUS (Hall)
Pl. 118, fig. 3

Graptolithus nitudus Hall, 1858, Geol. Survey Canada Rept. for 1857, p. 129.

Didymograptus nitidus Nicholson (part), 1868, Geol. Soc. London, Quart. Jour., vol. 24, p. 135.
(For more complete synonymy see Ruedemann, 1947, p. 339.)

Description.—Horizontal didymograptid in which stipes are remarkably straight after initial flexing in proximal ends of stipe. Sicula not observed in the specimens at hand. Thecae occur 12 to 13 per centimeter and are slightly curved to nearly straight. Thecae diverge from axis at approximately 40 degrees, and are approximately 1.5 to 1.6 mm. long and 0.4 mm. wide at the aperture, in characteristic specimens. Thecae in contact one-half to two-thirds their length. Apertural margin slightly concave and at right angles to axis of thecae, approximately 50 degrees to axis of stipe. A short mucro developed at lower margin in larger specimens of the species.

Discussion.—The Utah specimens are similar to the type specimens of the species, but have slightly more crowded thecae. *D. nitidus* is closely related to *D. patulus*, but is differentiated most easily in Utah specimens by variation in apertural characteristics. In *D. nitidus*, the apertural margin is normal to the axis of the thecae, but in *D. patulus*, the margin is at 50 or 60 degrees to the axis of the thecae. In most specimens of *D. nitidus* only short mucros are developed, but in *D. patulus* long mucros are common. *D. patulus* is slightly wider than *D. nitidus* in the specimens at hand.

Occurrence.—Didymograptus nitidus occurs in the Swan Peak quartzite of the Stansbury Mountains and in the Kanosh shale of the southern end of the Confusion Range. It occurs with *D. patulus* in localities in the Stansbury Mountains and in the Kanosh shale of the southern end of the Confusion Range. It occurs with *D. patulus* in localities in the Stansbury Range (B.Y.U. 10001, 10939), and with *D. bifidus* and *D. artus* in the Confusion Range (B.Y.U. 10941).

Didymograptus patulus (Hall)
Pl. 118, figs. 1,2,4,5

Graptolithus patulus Hall, 1858, Geol. Survey Canada, Rept. for 1857, p. 131.
Didymograptus patulus Matthew, 1893, Royal Soc. Canada, Proc. Trans., vol. 10, p. 98.
(For more complete synonymy see Ruedemann, 1947, p. 341, and Bassler, 1915, p. 434.)

Description.—Horizontal didymograptid diverging from a broad short sicula. Sicula 1.5 to 2.0 mm. long. First thecae branch approximately one-half way along sicula, second near the aperture. Thecae 12 to 13 per centimeter, range up to 2.6 mm. long but average 1.5 mm. long, and up to 0.6 mm. wide at the aperture. Thecae gently curved, diverging from axis of stipe at approximately 40 degrees then curving to approximately 60 degrees divergence. Aperture concave to slightly concave with a pronounced mucro at lower margin. Apertural margin approximately at right angles to trend of stipe or up to 120 degrees from direction of growth; usually at 50 or 60 degrees from trend of thecae. Many specimens with markedly thickened dorsal portion of stipe that may represent thickened nema up to 0.4 mm. thick in large specimens. Stipes widen from 0.7 mm. in proximal parts to 2.0 mm. approximately 15 mm. from sicula. Some expand to 2.4 or 2.5 mm. wide at widest part of stipe. Most specimens are fragmental, only four show initial portion of rhabdosome.

Discussion.—Didymograptus patulus is distinguished by its thecal count, apertural characteristics, and horizontal growth form. Methods of differentiating it from the associated *D. nitidus* have been summarized above.

Occurrence.—Didymograptus patulus occurs in the Swan Peak quartzite in the Stansbury Range (B.Y.U. locality 10001, 10939). Specimens have been collected from these localities by Mack Croft, John Teichert, Harold Bissell, and the writer.

Tentative Stratigraphic Zonation

Known stratigraphic occurrence of graptolite species in Utah is compared with graptolite zones established by Ross (1951) and Hintze (1951) in Table 1. It is apparent that early dendroid forms occur most frequently in zone G or earlier, and that various species of *Phyllograptus* occur in rocks of zone H. *Tetragraptus* and *Phyllograptus anna* are associated in rocks of zone J and K in the Ibex area. They have not been found elsewhere in the state. *Didymograptus bifidus* and *D. artus* occur in the upper part of the Kanosh shale and represent a characteristic graptolite assemblage of trilobite

TABLE 1—COMPARISON OF GRAPTOLITE OCCURRENCE AND TRILOBITE ZONES IN THE LOWER ORDOVICIAN OF WESTERN UTAH

Trilobite Zones (Hintze 1951)	Species of graptolites
N	*Didymograptus bifidus, D. patulus, D. nitidus*
M	*D. artus, D. bifidus*
L	no forms collected
K	*Phyllograptus anna*
J	*Tetragraptus similis, T. (?) quadribranchiatus, Tetragraptus* spp., *Phyllograptus anna*
H	*Phyllograptus loringi, P. ilicifolius grandis, P. ilicifolius stansburyensis, P. angustifolius pogonipensis, P. anna, Didymograptus artus*
G	*Dictyonema merriami, D. filiramus, D.* sp., *Desmograptus (?) utahensis, Didymograptus nanus*
F	no forms collected

zone N. In the Stansbury Mountains, *Didymograptus nitidus* and *D. patulus* occur in rocks tentatively called Swan Peak quartzite. It is possible that these forms are slightly older than *D. bifidus*, for they occur below *D. bifidus* in northeastern Utah (Clark, 1935, p. 241). If this is true, then *D. patulus* and *D. nitidus* would be representative of trilobite zone M. There is also the possibility that these horizontal forms are younger than *D. bifidus*, but evidence is inconclusive at the present time.

Graptolite zones established in the Deepskill area in New York by Ruedemann (1919, 1947, p. 123) and others seem to correlate well with those of Utah. From fragmentary evidence, one can recognize similarities, and also dissimilarities. Additional collections are needed before precise graptolite correlations can be made between Utah and New York sections.

The excellently exposed sequence of rocks in the southern Confusion Range may well be the most critical section of lower Ordovician rocks exposed in the Cordilleran area, for this series has been well zoned by Hintze (1951) on the basis of trilobites. In addition, graptolites, brachiopods, gastropods, ostracodes, and nautiloids occur interbedded throughout, making it possible to tie these various biologic zonations together in one standard section. A study of the possibility of composite zonation of these rocks is currently underway at Brigham Young University.

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JOURNAL OF PALEONTOLOGY, V. 32, NO. 5, P. 918–922, SEPTEMBER 1958

ON THE GEOLOGIC RANGE OF THE LABYRINTHODONT AMPHIBIAN *ERYOPS*[1]

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ABSTRACT—Comparison of the type of *Glaukerpeton avinoffi*, Carnegie Mus. No. 8539, with a specimen of *Eryops* sp. from the Dunkard series, lower Permian of Pennsylvania shows that the type specimen of *Glaukerpeton avinoffi* Romer, 1952 is referable to the genus *Eryops*. This helps to prove the existence of *Eryops* as early as Conemaugh time.

INTRODUCTION

REMAINS of the labyrinthodont amphibian *Eryops* are found in the lower Permian beds of Texas, New Mexico and Oklahoma, and in the lower Permian Dunkard beds of the eastern United States. In Texas, *Eryops* is known to range from the Pueblo formation (Romer, 1935) to the Vale and probably to the Choza (Olson, 1956), thus extending throughout at least most of the lower Permian. *Eryops* is found in both the Washington and Greene groups of the Dunkard series (Romer, 1952).

There has been some question as to the earlier occurrence of *Eryops*—whether or not it even existed in Pennsylvanian times and, if it did, how early. In 1908, Case described a dorsal vertebra without neural spine, a caudal neural spine, and three ribs collected by Dr. Percy E. Raymond from beds of Conemaugh age at Pitcairn, about fifteen miles east of Pittsburgh, Pennsylvania. Case (p. 235–236) referred these specimens to *Eryops*, the neural spine "without question," the vertebra "very probably," and the ribs "in all probability."

In 1952, Romer described *Glaukerpeton avinoffi*, based on Carnegie Mus. No. 8539, a specimen found in the city of Pittsburgh in a formation higher in the Conemaugh than the level from which Case's specimens were collected. Romer (p. 59) defined the genus and species as ". . . a rhachitomous amphibian with the characteristics of the Eryopsidae, face relatively long, lacrimal not in contact with frontal, no interfrontal, sculpture finer than in *Eryops*." Romer also noted (p. 59) that *Glaukerpeton avinoffi* had ". . . a considerable battery of small coronoid teeth."

Romer (1952, p. 60–61) considered the materials from Pitcairn assigned by Case to *Eryops* to be more correctly referable to the related genus *Glaukerpeton*. In addition to the dorsal vertebra, caudal neural spine and three ribs, Romer also tentatively assigned to *Glaukerpeton* several other specimens from Pitcairn: a distal neural spine ("undetermined amphibian," according to Case), seven chevrons (assigned to the Diadectidae by Case), fragments of pubis and ischium (assigned by Case to either the Pelycosauria or the Diadectidae), a sacral rib (identified by Case as the ilium of an undetermined reptile), and other fragments. That the sacral rib showed a "complete difference in detail" from that of *Eryops*, despite general similarity, seems to have been one of the chief reasons for Romer's reassignment of Case's specimens. Fragmentary remains of a rhachitome from another locality in the Conemaugh of Allegheny County, Pennsylvania were also identified by Romer as probably pertaining to *Glaukerpeton*.

If the materials from Pitcairn do not belong to *Eryops*, there is no evidence for the occurrence of this genus in the Conemaugh, and, indeed, Romer (p. 60) thought it improbable that *Eryops* was in existence that early.

In 1953, Messrs. John J. Burke and William E. Moran collected the greater part of the crushed skull of a labyrinthodont amphibian from a layer of fresh-water limestone high in the Greene group, Dunkard series, one mile north of Ned, in the southwesternmost part of Greene County, Pennsylvania. The Dunkard series is probably roughly equivalent in age to the Wichita

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group, lower Permian of Texas (Romer, 1952, p. 100). Resemblance of this specimen, U.S.N.M. No. 21860, to the type of *Glaukerpeton avinoffi* is readily apparent. The most immediately obvious points of similarity are the small size (as compared to, say, typical examples of *Eryops megacephalus*) and delicate sculpture of both specimens. This resemblance, in view of the disparity in age and the fact that U.S.N.M. No. 21860 seems to be definitely referable to *Eryops*, has prompted a close comparison of the two.

UNITED STATES NATIONAL MUSEUM SPECIMEN NO. 21860

U.S.N.M. No. 21860 is a dorsoventrally flattened, somewhat distorted, partial skull on a slab and counterslab. Nothing is preserved of that part of the skull posterior to the parietal foramen. The slab contains, in dorsal view, the two frontals (with the right frontal almost complete); parts of the premaxillae, right maxilla, parietals (anterior to the level of the parietal foramen), right postfrontal, and vomers; traces of the sphenethmoid, pterygoids, and right palatine; and an impression of the left postfrontal. On the counterslab may be seen parts of the vomers and left postfrontal in ventral view, and impressions of most of the elements visible on the slab. Parts present on slab or counterslab that are not also preserved in impression were uncovered by the use of hand tools after the splitting of the block. This is particularly true of the anterior parts of the frontals (slab) and the posterior parts of the vomers (counterslab).

Comparison with U.S.N.M. No. 6721, a specimen of *Eryops megacephalus* from Texas, and with Sawin's (1941) description of the skull of *E. megacephalus* shows that U.S.N.M. No. 21860 is referable without question to the genus *Eryops*. The general contour of the skull, as far as it can be made out, is the same as in *Eryops*. As in *E. megacephalus*, U.S.N.M. No. 21860 shows a distinct "step" in the vomer, so that the ventral surface of the posterior part occupies a more dorsal plane than does the ventral surface of the anterior part. As in *Eryops*, the vomer is quite thick where it borders the internal naris.

The most diagnostic feature of U.S.N.M. No. 21860, however, is the clear indication of the presence of an interfrontal bone. The frontals diverge from one another anteriorly, leaving a broad, U-shaped space between them which could have been occupied only by an interfrontal ("internasofrontal" of Sawin and others). The appearance of the skull roof in this region is very similar to the appearance of the corresponding portion of Carnegie Mus. No. 8532, a specimen of *Eryops* cf. *megacephalus* from the Greene group, Dunkard series of Monongalia County, West Virginia (Romer, 1952, pl. 2, fig. 1). Romer (*ibid.*, p. 63) considered Carnegie Mus. No. 8532 to be an immature individual; perhaps the same is true of U.S.N.M. No. 21860, and this may explain the lack of preservation of the interfrontal in these specimens. The presence of an interfrontal bone is rare in the Labyrinthodontia; Romer (1947) figures an interfrontal in the eryopsids *Eryops* and *Osteophorus*, in the trematopsid *Mordex*, in the trematosaurid *Trematosuchus*, and in the capitosaurid *Kestrosaurus*. *Trematosuchus* and *Kestrosaurus*, with their elongate snouts, Triassic age, and occurence, so far as is known, only in South Africa, need not be considered. *Mordex* is known only from the Pennsylvanian of Europe, and, besides, its interfrontal is *very* small. *Osteophorus*, from the lower Permian of Europe, is easily differentiated by, among other things, its narrower muzzle from its possible relative, *Eryops* (Romer, 1947, p. 139); U.S.N.M. No. 21860 has as broad a muzzle as has *E. megacephalus*.

U.S.N.M. No. 21860 is referable to *Eryops* only. There are, nevertheless, two points of difference from typical described specimens of *Eryops*—at least *E. megacephalus:* (1) more delicate ornamentation of the dermal roofing bones, and (2) smaller size. The second point of difference is perhaps due to immaturity, and possibly the first is a function of the second; it is certainly true that the ornamentation becomes coarser with increase in size in, for example, *Alligator*.

Degree of fineness of sculpture is not an easy character to measure, but, roughly, there are sixty or so pits per square inch on the right frontal, on a level with the center of the orbit, in U.S.N.M. No. 21860, as compared with about twenty-five pits

per square inch in the same region in U.S.N.M. No. 6721, a specimen of *Eryops megacephalus* about average in size (according to table published by Sawin, 1941).

Due to the distorted nature of U.S.N.M. No. 21860—with the frontals displaced to the left and probably somewhat anteriorly—comparison of sizes is difficult. Interorbital widths may, however, be compared. The distance between orbits in U.S.N.M. No. 21860 is about 70 mm., as compared with an interorbital width of 90 mm. for a specimen about the median in size of the nine specimens of *Eryops megacephalus* measured by Sawin (1941, p. 410). Sawin (*loc. cit.*), however, reports interorbital widths in *E. megacephalus* ranging all the way from 70 mm. (total skull length: 386 mm.) to 110 mm. (total skull length: 525 mm.). Romer (1952, p. 62–63) describes fragmentary skulls of *Eryops* cf. *megacephalus* from the Dunkard series of Ohio and West Virginia with estimated total skull lengths of 335 mm. and 320 mm.; these estimates suggest interorbital widths of considerably less than 70 mm. It may be seen from this that, while the size of U.S.N.M. No. 21860 is less than the average for known specimens of *Eryops*, it falls easily within the range in size of that genus.

CARNEGIE MUSEUM SPECIMEN NO. 8539

In considering Carnegie Mus. No. 8539, the type of *Glaukerpeton avinoffi*, it might be best to proceed by discussing *seriatim* the characters listed in Romer's diagnosis of the genus and species (1952, p. 59–60).

The characters ". . . face relatively long, lacrimal not in contact with frontal . . ." are, of course, characters found in *Eryops* and constitute no barrier to assignment to that genus.

Romer based the character ". . . no interfrontal . . ." on his interpretation of the broken and dislocated elements of the skull roof. He figured these elements (1952, fig. 1) both as they actually lie in the specimen and in a restoration. He noted (p. 58) that ". . . the posterior portions of both frontals are in position. A piece of bone lying well ahead of the right frontal fits perfectly onto the articulated portion and hence is the anterior part of that bone" and stated of this piece of bone that "When articulated, the median margin lies close to the midline and hence the interfrontal bone characteristic of *Eryops* was not present." This latter statement was based upon Romer's use of full-sized cut-outs from photographs of the pieces. But, considering the similarity of U.S.N.M. No. 21860 to Carnegie Mus. No. 8539 in size (both have an interorbital width of about 70 mm.) and fineness of sculpture (both have about sixty pits to the square inch in the same region of the frontal), and the fact that U.S.N.M. No. 21860 undoubtedly had an interfrontal, it would seem worthwhile to make a fresh search for the interfrontal in the genoholotype of *Glaukerpeton*.

In addition to being broken, some of the elements and pieces of elements of the roof of Carnegie Mus. No. 8539 are far removed from their original positions. I have carefully compared Romer's drawing (1952, fig. 1A) with the specimen and am in agreement with his identifications of the individual pieces except in the case of one element, the one he labeled as "right nasal."

I have prepared a paper cut-out of a full-sized camera lucida drawing of the anterior one of the two pieces of the right frontal. As Romer did, I interpret the edge that faces posteriorly and medially as the fragment lies in the specimen as the edge along which it was originally joined to the posterior piece. Fitting this anterior fragment to the posterior piece, I find that the posterior half of the medial edge of the fragment does indeed lie nearly along the midline of the skull, but anterior to this there is a decided indentation, reaching almost halfway across the fragment, forming a step which could have comfortably received the posterolateral portion of an interfrontal. Further, that part of the fragment immediately adjacent to the portion of the medial edge that does lie along the midline is in the form of a smooth shelf whose dorsal surface lies 1–2 mm. below the dorsal surface of the rest of the fragment. Possibly this shelf underlapped the posterolateral edge of an interfrontal; it seems unlikely that the right frontal would have underlapped the left to any appreciable extent. It is, of course, also possible that this shelf was originally covered by a sculptured

"layer" lost post-mortem, and it is further possible that the shelf underlay an area of incomplete ossification.

The element Romer labeled as "right nasal" lies, in the specimen, anterior and medial to the anterior fragment of the right frontal, on which it abuts. As far as I can make out, there seems to be no reason for believing that this abutment does not represent an original articulation; there are, as a matter of fact, signs of incipient fusion in restricted areas along this abutment. It is difficult, therefore, to see how this element could be a right nasal. The nasal in Romer's reconstruction (1952, fig. 1B) lies anterior and *lateral* to the frontal—as does the nasal in *Eryops*. I consider it much more likely that this element is the interfrontal. It fits into the frontal as an interfrontal would, with its posterolateral margin lying against the anterior two-fifths or so of the frontal—as in *Eryops* (Sawin, 1941, fig. 1). And, again as in *Eryops*, the element is approximately four-fifths as long as the frontal and does not extend laterally beyond the anterior apex of the latter. Romer interpreted fragments immediately to the left of this element as pieces of the left nasal. Although I feel that the posteriormost of the fragments so identified may really be a part of the left lacrimal, the identification of any or all of these fragments as belonging to the left nasal would be in accord with my interpretation; in *Eryops*, the posterior portions of the nasals flank the interfrontal. The right nasal seems not to have been preserved. We may say, then, that the amphibian represented by Carnegie Mus. No. 8539 probably had an interfrontal, and that the interfrontal is present in the specimen as the element labeled "rn" in Romer's figure.

It has been pointed out that the sculpture pattern of Carnegie Mus. No. 8539 is no finer than that of U.S.N.M. No. 21860. There is, therefore, no longer any basis for the differentiation of the former on the character " . . . sculpture finer than in *Eryops*."

Although he did not include his observation in his definition of *Glaukerpeton avinoffi*, Romer (1952, p. 59) noted that "At the far end of the slab [Carnegie Mus. No. 8539] are two lower jaw fragments; the inner surface of the larger fragment faces upward and can be seen to bear (in contrast with *Eryops*) a considerable battery of small coronoid teeth." In 1947 (p. 133) Romer described the coronoids of *Eryops* as " . . . almost toothless although there are small denticles on the posterior bone of the series." This remark was based mainly on study of the typical species, *E. megacephalus*. Sawin (1941, p. 430 and pl. 5B) described and figured small denticles on the medial surface of the posterior coronoid of *E. megacephalus*. His figure shows these denticles to be fairly numerous, but not so numerous as in Carnegie Mus. No. 8539. Langston (1953, p. 378), however, reports of a specimen of the New Mexican species, *E. grandis*, that "A dense shagreen of denticles overlies all three coronoids and completely obscures the intercoronoid sutures." Inspection of Langston's drawing (fig. 11) shows the denticles to be as numerous and as densely packed as the coronoid denticles of Carnegie Mus. No. 8539.

THE GEOLOGIC AGE OF ERYOPS

Since, upon comparison with U.S.N.M. No. 21860 and with other specimens referable to *Eryops*, it can be seen that there remains no feature that might form a barrier to the assignation, I suggest that Carnegie Mus. No. 8539 be referred to *Eryops* and that the generic name *Glaukerpeton* be abandoned. On the basis of the stratigraphic occurrence of Carnegie Mus. No. 8539, it can be said that the genus *Eryops* was in existence as early as the Conemaugh. In possible corroboration, it may be pointed out that some, at least, of the specimens from Pitcairn, Pennsylvania might be reassigned to *Eryops*, where Case believed them to be belong.

Romer (1952, p. 102–103) has analyzed the Dunkard facies of the early Permian fauna and flora as indicating " . . . a flat, well-watered coastal region with abundant swamps and lagoons. . . . " Perhaps Carnegie Mus. No. 8539 and U.S.N.M. No. 21860 represent a distinct species of *Eryops*, *E. avinoffi*, possibly a primitive form able to linger on late into the early Permian because of the persistence in the region of an environment little changed from that of late Pennsylvanian times.

ACKNOWLEDGMENTS

I am grateful to Messrs. John J. Burke and William E. Moran who collected U.S.N.M. No. 21860 and who conducted me to the site whence it came. Thanks are also due to Drs. J. LeRoy Kay and M. Graham Netting for the loan of Carnegie Mus. No. 8539.

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THE EDRIOASTEROID *LEPIDODISCUS SQUAMOSUS* (MEEK & WORTHEN)

ROBERT V. KESLING AND GEORGE M. EHLERS

ABSTRACT—A specimen of *Lepidodiscus squamosus* (Meek & Worthen) believed to be the holotype has been found at the Museum of Paleontology of the University of Michigan. Because *L. squamosus* is the type species of *Lepidodiscus*, this specimen is of particular interest. Certain details can now be added to Meek & Worthen's original description. The ambulacral plates are more numerous than shown by Meek & Worthen in their drawing published in 1873, five years after the species was described. In some parts of the ambulacra the plates are irregular, but in most parts they are arranged in cycles of six, of which two plates do not extend to the outside edge of the ambulacrum. The peripheral plates are set at a steep angle, imbricating, and not fused into a ring, as in other species presently assigned to *Lepidodiscus*. The peristome covering plates form a bulge in the right posterior region, and they have collapsed along a line. This feature is similar to that pointed out by Hecker in 1940 in *Lepidodiscus ephraemovianus* (Bogolubov). The position of the structure corresponds to that of the hydropore in *Edrioaster bigsbyi* (Billings), and the bulge may contain some kind of hydropore.

INTRODUCTION

DISCOVERY of a specimen of *Lepidodiscus squamosus* (Meek & Worthen) which we believe to be the holotype permits a restudy of the species. Insofar as we know, this is the only specimen ever found of *L. squamosus*, the type species of *Lepidodiscus*. Although poorly preserved, it clearly shows certain characteristics different from those in edrioasteroids now assigned to other species of *Lepidodiscus*.

At least 10 years ago, and perhaps as long as 30 years ago, an exhibit of echinoderms was set up in the Hall of Evolution in the Museum of Paleontology at the University of Michigan. Two edrioasteroids were included in this exhibit. The one which is the subject of this paper was accompanied by a label reading:

LEPIDODISCUS SQUAMOSUS
MEEK AND WARTHIN
SILURIAN
5420 CRAWFORDSVILLE, IND.

In the course of our study of edrioasteroids, we examined this specimen. To our knowledge, we were the first to open the case housing the exhibit since it was prepared. The reference to Silurian age is puzzling, since no Silurian strata are exposed near Crawfordsville, Indiana. The famous collecting locality there is an outcrop of Mississippian Edwardsville formation. The coauthor of the species is Worthen, not Warthin as given on the label.

Since a catalogue number accompanied the specimen, we checked the catalogue card in the Museum of Paleontology, and found the following information:

5420 Agelacrinus (Lepidodiscus) squamosus M & W.
Niagara
Crawfordsville, Ind.
Rominger

It contains no indication that the cataloguer recognized this specimen as a type.

The entry "Rominger" indicates that this edrioasteroid was part of Dr. Carl Ludwig Rominger's extensive fossil collection. Most of his specimens are now in the Museum of Paleontology. In 1864, when Dr. Rominger was Assistant Curator in the Museum of Geology, Zoology, and Botany of the University of Michigan, he deposited most of his large collection of fossils from Europe in the Museum.

In his history of the Museum of Paleontology, L. B. Kellum states (1956, p. 1492–1493):

> On June 27, 1865, the Regents received a communication from Winchell "in relation to the enlargement and improvement of the Museum and the employment of Dr. C. Rominger as Curator of the Museum of Geology, Zoology and Botany, to be charged with the duty of laboring for the increase and preservation of the collections in this department" . . . A sum of $300 was appropriated "for the purpose of

> employing Dr. Rominger to make collections in Natural History, for the use of the Museum . . . ." With this sum he made twelve collections, comprising 320 species of fossils from Ordovician, Silurian, Devonian, and Mississipian strata in Indiana, New York, Michigan, and Ontario. Nevertheless, in September, 1866, the Committee on the Museum recommended that his salary as Assistant Curator of the Museum be discontinued.

Thus, it appears quite likely that the specimen of *Lepidodiscus squamosus* was collected in 1865 by Dr. Rominger, and was loaned to Meek and Worthen three years later for description. Nevertheless, in 1881 Rominger had the specimen in his possession and definitely regarded it as his property. In the Museum of Paleontology there is a bound journal written in Dr. Rominger's German script. One section of this journal is entitled "Petrefactorum Catalogus / Merz 1881," and includes the following entry on page 37: "Agelacrinus squammosus [sic] / Subcarb. Crawfordsville . . . 1 Stk." (Dr. Rominger often wrote partly in German and partly in English, and "Stk." undoubtedly is the abbreviation of the German "Stück," meaning "specimen"). In the same journal, under the section headed "Catalogue of Collection deposited in the University Museum as a loan with the view of selling it to the Museum if the necessary funds are appropriated for the purpose," Rominger listed on page 215, "Agelacrinus squamosus M. & Worthen / Crawfordsville . . . 1 Stk."

Negotiations for the purchase of Rominger's European collection by the University began in 1864, when he first deposited it at the Museum. During succeeding years, Rominger added numerous specimens from Michigan and nearby states to his collection. On January 1, 1888, the University started renting Rominger's collection for $125 per half year. At last, in December of 1891, after nearly 28 years of negotiation and delay, the University purchased the fossils for $5,000. We assume that the edrioasteroid here described came into the possession of the University in this transaction.

It is also of interest that Rominger, in his "Petrefactorum Catalogus," listed many other echinoderms from "Subcarb. Crawfordsville." They include numerous specimens of 27 identified species, in addition to several unidentified species. Of these, many are catalogued in the Museum of Paleontology, including the holotypes of the rare echinoids *Lepidestes coreyi* and *Oligoporus coreyi* described by Meek & Worthen (1868*b*, p. 525; 1870, p. 34), and a hypotype of the crinoid *Onychocrinus exculptus* Lyon & Casseday figured by Meek & Worthen (1873, pl. 14, fig. 4). Regarding the last, Rominger wrote in his "Petrefactorum Catalogus": "original exemplar figured by Worthen."

Although Meek & Worthen in their several publications do not mention Rominger as the collector of specimens they described, it appears that Rominger loaned some of his choice echinoderms to them for study and description. Of course, it is possible that Meek or Worthen obtained the specimens which they described from another source, and traded them to Dr. Rominger for specimens in his collection. In those days, excellent specimens from one locality were swapped for those from another to build up a large collection, and holotypes commanded little respect except as prime trading material.

Meek & Worthen (1870, p. 34) say in their original description of *Oligoporus coreyi*, "The specimen from which the description was made out belongs to Mr. Corey, of Crawfordsville, Ind., to whom we have dedicated the species." If we knew how the holotype of *Oligoporus coreyi* came into Rominger's possession, perhaps we would know more of the history of the holotype of *Lepidodiscus squamosus*.

The photography of this poorly preserved

EXPLANATION OF PLATE 119

FIGS. *1–3*—*Lepidodiscus squamosus* (Meek & Worthen). Holotype, UMMP No. 5420. *1*, natural size, coated with ammonium chloride. *2*, enlarged, photographed when submersed in xylol to show the plates. *3*, reproduction of Meek & Worthen's figure (1873, pl. 16, fig. 1) in their orientation, slightly reduced to correspond to their measurement (1873, p. 514).

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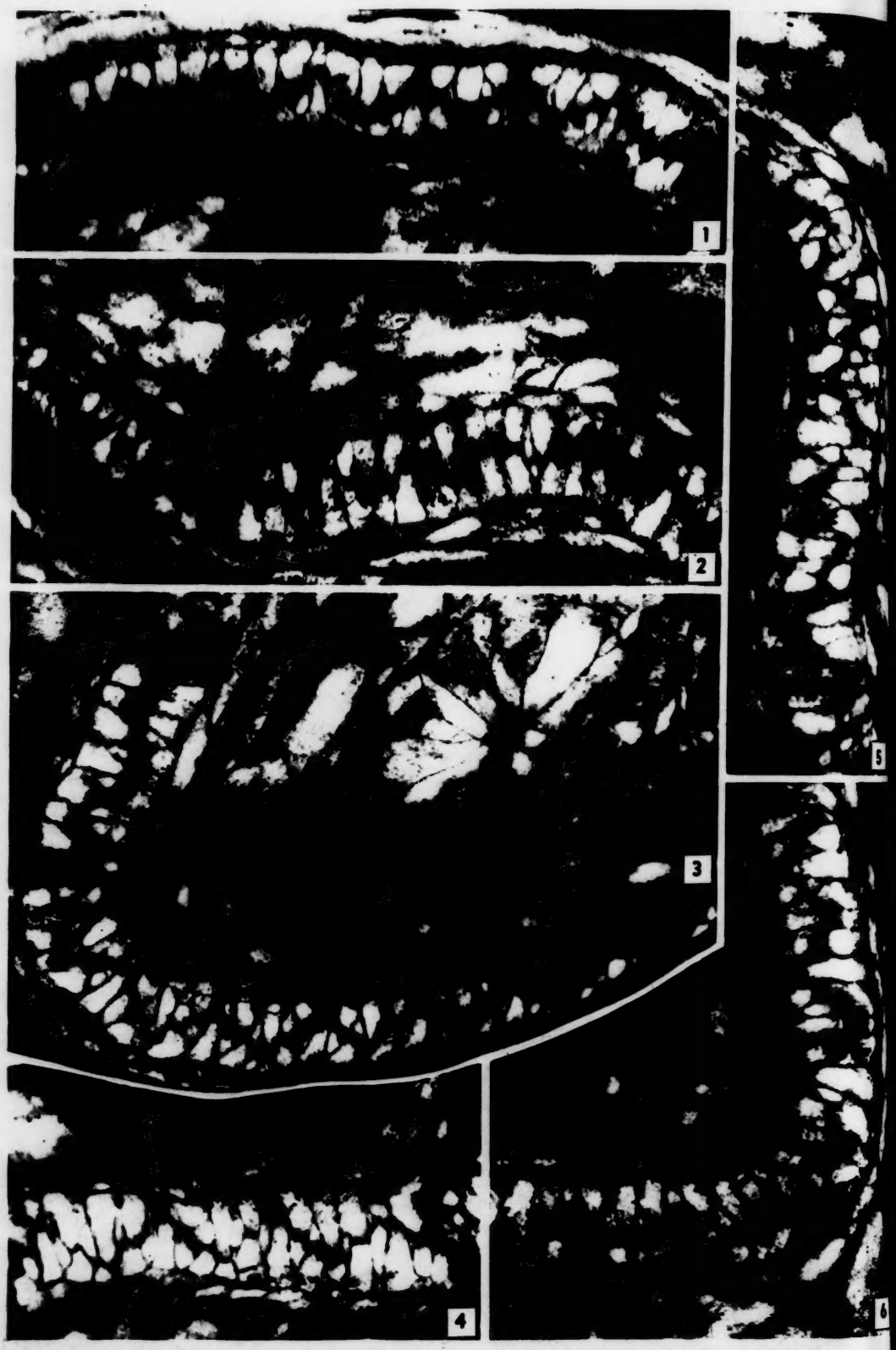
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specimen presented many problems. Because the plates were worn in many parts of the ambulacra, a coating of sublimate hid many significant details. We found, after several trials, that the best results were achieved with the specimen immersed in xylol. Because of the sharp contrast between the color of the plates and the color of the matrix, it was necessary to use a film of very low contrast to show the complete specimen to advantage. However, film of greater contrast was used to show details of the ambulacral plates.

We greatly appreciate the efforts of Dr. Porter M. Kier of the United States National Museum, Dr. Carlton Condit of the Illinois State Museum, and Dr. Charles Collinson of the Illinois State Geological Survey for searching through the collections at their institutions for specimens of *Lepidodiscus squamosus*.

SYSTEMATICS

Phylum ECHINODERMA
Subphylum PELMATOZOA
Class EDRIOASTEROIDEA Billings, 1858

There has been some confusion in literature on the origin of the name of this class. The first reference we have found that proposes such a designation is by Billings, 1858, p. 85, who wrote:

> I have placed *E.* (*Edrioaster*) *Bigsbyi* in the order Asteriadae, because its structure appears to me to be more like that of the Star-fishes than that of the Cystideae. None of the Cystideae have ambulacra whose pores penetrate through the covering of the body, and therefore all such genera as *Edrioaster*, *Agelacrinites* and *Hemicystites*, belong to a very different division of the Echinodermata. When we know more of their structure it is probable that they will be arranged as a sub-order, for which the name *Edrioasteridae* would be appropriate, as it would suggest their sessile condition on the one hand, and on the other their affinity to the Asteriadae.

Family AGELACRINITIDAE Clarke, 1901

S. A. Miller (1877, p. 65) used "Order Agelacrinidae" to include *Agelacrinus*, *Edrioaster*, and *Hemicystites*. Later (1889, p. 216) he used "Order Agelacrinoidea" for the families "Agelacrinidae" and "Hemicystidae." In 1899 (p. 57) Jaekel claimed authorship of this spelling, writing "Fam. Agelacrinidae m." Bather (1900*a*, p. 207) and others, including Piveteau (1953, p. 651), also used the family name "Agelacrinidae." Miller's "Agelacrinidae" and "Agelacrinoidea" were based on the stem of the much used but erroneous change in the spelling of *Agelacrinites* to *Agelacrinus*. The correct name of the genus is that which Vanuxem (1842, p. 158) originally proposed—*Agelacrinites*. Because Miller's names are not based on the correct generic stem, he cannot be regarded as the author of the suprageneric taxon.

In 1901 on page 183 and again on page 198, J. M. Clarke referred to the "family Agelacrinitidae." He also called attention to the erroneous spelling of *Agelacrinites*. In 1935 (p. 2) R. S. Bassler, evidently unaware of Clarke's correct family name, proposed "Agelacrinitidae, new name." we believe Clarke was the first to use the correct stem and is the author of the family.

The family is used here as emended by Bassler (1935, p. 2) and further restricted by him (1936, p. 15) to include *Agelacrinites*, *Cooperidiscus*, *Discocystis*, *Isorophus*, *Isorophusella*, *Lepidodiscus*, *Thresherodiscus*, and *Ulrichidiscus*. The family, as now restricted, includes edrioasteroids with a single row of

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EXPLANATION OF PLATE 120

All figures ×10, retouched

FIGS. *1–6*—*Lepidodiscus squamosus* (Meek & Worthen). Holotype, UMMP No. 5420. *1*, central part of ambulacrum III, showing fairly regular cyclic arrangement of ambulacral plates. *2*, distal part of ambulacrum V. *3*, proximal and central parts of ambulacrum I, the anal pyramid, and (at the right) the end of ambulacrum V, showing the small interambulacral plates bordering the ambulacra and anal pyramid. *4*, proximal part of ambulacrum IV. *5*, proximal part of ambulacrum III; note the irregularity of plates where the ambulacrum recurves. *6*, recurved part of ambulacrum II, showing insertion of several plates in addition to the normal cycle at the bend.

flooring plates in each ambulacrum and numerous covering plates of the peristome.

Genera are distinguished by the presence of branching in the ambulacra, the curvature of the ambulacra, the width of the ambulacra, and the mosaic or imbricating character of the interambulacral plates.

Genus LEPIDODISCUS Meek & Worthen, 1868*a*

Type species.—By monotypy, *Agelacrinites* (*Lepidodiscus*) *squamosus* Meek & Worthen, 1868*a*, p. 357.

The generic name was first used by Meek & Worthen (1868*a*, p. 357) for a subgenus of *Agelacrinites*. They compared their species with *Agelacrinites hamiltonensis* Vanuxem, the type species, and noted that, whereas *A. hamiltonensis* had ambulacra IV and V curved to the right and mosaic interambulacral plates, their species had only ambulacrum V curved to the right and imbricating interambulacral plates. They concluded (1868a, p. 358):

> It therefore certainly seems to us doubtful whether species differing in two such important characters as these are strictly congeneric. If they are not, then a new generic name should be applied to our species, and the others agreeing with it in these characters, in which case we would propose to designate this group of species under the name *Lepidodiscus* . . . . At least we should think they ought to be separated subgenerically.

As now employed, the genus *Lepidodiscus* includes, in addition to the type species, *L. alpenensis* Bassler, 1936, *L. beecheri* (Clarke, 1901), *L. buttsi* (Clarke, 1901), *L. ephraemovianus* (Bogolubov, 1926), *L. lebouri* Sladen, 1879, and *L. milleri* Sharman & Newton, 1892. These species have long, curved ambulacra, of which ambulacra I–IV curve to the left and ambulacrum V to the right, and numerous, strongly imbricating interambulacrals. The genus ranges from Middle Devonian to Mississippian.

LEPIDODISCUS SQUAMOSUS (Meek & Worthen, 1868*a*)
Pl. 119, figs. 1–3; pl. 120, figs. 1–6; text-fig. 1

Agelacrinites (*Lepidodiscus*) *squamosus* MEEK & WORTHEN, 1868*a*, p. 357–358; 1873, p. 513–515, pl. 16, fig. 1.
Lepidodiscus squamosus CLARKE, 1901, p. 184, 188–193, 198. BASSLER, 1935, p. 8; 1936, p. 20, pl. 1, fig. 17; 1938, p. 123. BASSLER & MOODEY, 1943, p. 207. SHIMER & SHROCK, 1944, p. 131, pl. 49, fig. 21.
Agelacrinus squamosus MILLER, 1889, p. 222.
Agelacrinites squamosus JAEKEL, 1899, p. 51.

THE SPECIMEN

There are several reasons for considering this specimen to be the holotype. In 1873 (p. 514), Meek & Worthen repeated their previous (1868*a*, p. 357) statement, "The only specimen of this species we have seen is somewhat crushed and distorted. . . ." No other specimen has been mentioned in literature since that time.

Meek & Worthen (1868*a*, p. 357; 1873, p. 514) give the greatest diameter of the specimen they describe as 1.70 inches; this is the size of UMMP No. 5420. Their figure (1873, pl. 16, fig. 1, here reproduced as pl. 119, fig. 3) shows the right anterior part of the specimen broken off; the right anterior part is missing in UMMP No. 5420. The figure also shows ambulacrum IV broken off before it completely recurves; ambulacrum IV in UMMP No. 5420 is broken off at the corresponding place. Their figure further shows the distal parts of ambulacra I, II, and III lying on or near the periphery; these ambulacra in UMMP No. 5420 extend to the periphery. In several other details, Meek & Worthen's figure matches our specimen, as in the shape of the ambulacra, the position of the analy pyramid at the left side of the posterior interambulacrum, and the termination of ambulacrum V just below the anal pyramid.

In a few details, Meek & Worthen's figure of the type differs from UMMP No. 5420. In the anterior region, lying between the distal part of ambulacrum III and the periphery, they show a continuation of ambulacrum IV. In UMMP No. 5420 no trace of ambulacrum IV is exposed at the surface in this part of the specimen; instead, there are only upturned peripheral plates, but the broken edge of the specimen shows a cross section of ambulacrum IV, suggesting that the peripheral plates in this region were compressed and shoved over the top of the distal part of the ambulacrum. Meek & Worthen show ambulacrum I terminating at about the midventral part of the periphery. In UMMP No. 5420 ambulacrum I

extends farther, and terminates below the recurved part of ambulacrum V. In addition, in Meek & Worthen's figure the center lines of ambulacra I and II extend separately into the peristomial region, but in our specimen these lines join at the left side of the peristomial region.

In view of the crushed and distorted nature of UMMP No. 5420, it would be surprising, indeed, if an artist produced a photographic likeness. We are convinced, by the many points in which our specimen, UMMP No. 5420, agrees with the drawing given by Meek & Worthen, that it is the holotype.

Dr. Charles Collinson searched for specimens of *Lepidodiscus squamosus* at the Illinois State Geological Survey, Dr. Carleton Condit at the Illinois State Museum, and Dr. Porter M. Kier at the United States National Museum, but none could be found. We believe this is the only known specimen of the species.

The specimen is incomplete, as mentioned above. Furthermore, its upper surface was evidently displaced toward the left posterior edge. At this place, ambulacra I, II, and III lie along the periphery, as seen in an oral view, but the peripheral plates are still preserved under the edge, where they are hidden in this view.

The matrix is a very dark limestone with numerous pelmatozoan columnals and fragments. We did not attempt to remove it to uncover the aboral surface of the specimen because of the fragile nature of the parts exposed on the oral side. Although we spent many hours in cleaning the specimen, we removed very little matrix. Most of our work consisted of uncovering the small plates along the edges of the ambulacra.

AMBULACRA

The general curvature of the ambulacra is given by Meek & Worthen (1868a, p. 357; 1873, p. 513, 514). To their description should be added that a short distance from the peristomial region ambulacra I, II, III, and IV curve to the right before strongly recurving to the left, and that ambulacrum V curves to the left before strongly recurving to the right.

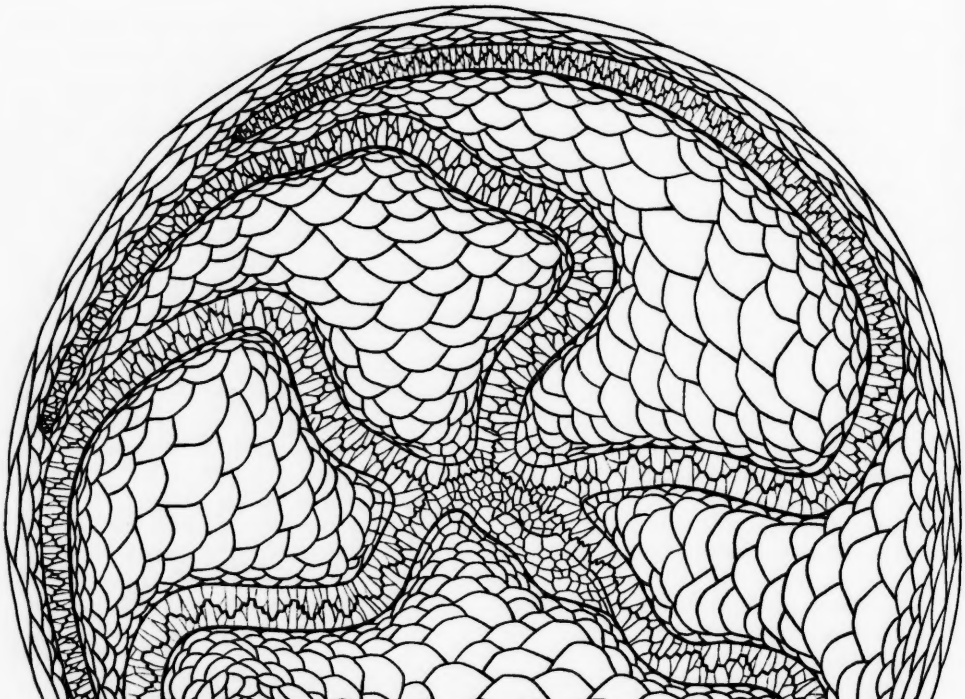
In no part of the specimen are the flooring plates exposed to show their shape or arrangement. At the broken end of ambulacrum IV the flooring plates are thick and lie rather close to the covering plates.

AMBULACRAL COVERING PLATES

Meek & Worthen (1868*a*, p. 357; 1873, p. 514) describe the ambulacra: ". . . each composed of two zigzag rows of very small pieces, with some irregular ones apparently not belonging properly to either row."

As can be seen in the photographs (pl. 119, fig. 2; pl. 120, figs. 1–6), the conspicuous feature of the arrangement of ambulacral covering plates is a prominent zigzag central line dividing those of one side from those on the other. This zigzag line begins near the peristomial region and extends to the end of each long arm. Each limb of the major zigzag line is itself conspicuously serrate. In contrast to the covering plates of the peripstome and the nearby parts of the ambulacra, some which have their edges serrate at the central line (see text-fig. 1 and pl. 119, fig. 2), the other plates in the ambulacra are not serrate at the central line (pl. 120, figs. 1–6). Instead, each angle in the central line meets a line dividing two of the ambulacral plates on one side or the other, so that each plate is angular but not indented. In other words, each angle of the central line is formed on one side by the acuminate end of one plate and on the other side by the edges of two plates.

In some parts of each ambulacrum the covering plates are somewhat irregular, but throughout most of the ambulacrum, particularly the distal half, they are regularly cyclic. The plates on each side of the zigzag central line occur in cycles of six, with few exceptions (pl. 120, fig. 1). In each cycle, the first, second, fourth, and sixth plates extend from the central line to the outside edge of the ambulacrum. The first is short and quadrate; the second is intermediate in length and irregularly hexagonal, its outer part subquadrate and its inner part acuminate; the fourth plate, the longest in the cycle, is subquadrate except that the inner corners are beveled; and the sixth plate is a mirror image of the second. The third plate is subrhombic, inserted between the second and fourth plates, with its inner apex forming a serration on the central line of the ambulacrum. The fifth plate is a mirror image of the third, lying on the opposite side



TEXT-FIG. *1*—Hypothetical reconstruction of *Lepidodiscus squamosus* (Meek & Worthen) based on the holotype and only known specimen. The small plates at the peripheral edge, lying on the nearly vertical face of the large peripheral plates, have not been indicated.

of the long fourth plate. In most cycles, the subrhombic third and fifth plates do not extend to the outside edge of the ambulacrum, but terminate along the side of the fourth plate. The plates on the other side of the ambulacrum are arranged in similar cycles but offset by half a cycle, so that the first plate on one side lies directly opposite to the fourth plate on the other side.

In the proximal part of each ambulacrum and at the place where it rather abruptly recurves, extra plates are irregularly inserted in the cycles (pl. 120, figs. 3,5,6).

Meek & Worthen (1868*a*, p. 357; 1873, p. 514) also state that the ambulacra are "apparently not provided with *open* ambulacral furrows, the rows of minute plates on each side, apparently closing up and interlocking. There appear, however, to be pores arranged along them in a zigzag row between the plates." There is no evidence that the plates interlocked, if by that term is meant that the free movement of plates was constrained. Instead, the plates of one side abut against those of the other side, fitting evenly against them and leaving no interstices. We can

discern no pores along the central lines of the ambulacra.

This pattern of plates may be unique. Insofar as known, in other species presently assigned to *Lepidodiscus* the ambulacral plates are more nearly alike, and, with few exceptions, vary only in a gradual decrease in size toward the distal end of the ambulacrum. In these species, the acuminate ends of the plates on one side alternate with those on the other side, forming a serrate central line the length of the ambulacrum. It may be mentioned here, however, that *Discocystis laudoni* Bassler, as shown in the original figures (1936, pl. 3, figs. 7–8), also has a prominent zigzag line along each ambulacrum, but precise details of its plate pattern are not known.

INTERAMBULACRAL PLATES

Meek & Worthen (1868*a*, p. 357; 1873, p. 514) state:

> Disc composed of large, thin, irregular, strongly squamose or imbricating plates, the imbrication being inward from the periphery, that is, the inner edge of each plate laps upon the outer edge of the next. . . . Ovarian ? pyramid . . . forming a depressed cone, around the base of which there are numerous small, short, but comparatively wide imbricating disc plates.

Some of the interambulacral plates are worn and a few are missing. As can be seen in the photograph (pl. 119, fig. 2) and as indicated in the restoration (text-fig. 1), the plates are distinctly imbricating, overlapping toward the center with three exceptions. First, small imbricating plates lap up to both the inner and outer edges of the ambulacra (pl. 120, figs. 2–5); those along the inner edges of the ambulacra reverse the general direction of imbrication. Second, the interambulacral plates in the region of the anal pyramid are small and overlap toward the center of the pyramid (pl. 120, fig. 3). Third, the interambulacral plates near the peristomial region are small and nearly mosaic, imbricating very little if at all (pl. 119, fig. 2).

The interambulacral plates are very large in the center of each interambulacrum and decrease abruptly towards the edges of the ambulacra and towards the anal pyramid. Those in the distal region differ very little from the plates in the peripheral ring. The only difference we can point out is that the plates in the peripheral ring are set at a much steeper angle, being nearly vertical, whereas the interambulacral plates are nearly horizontal.

ANAL PYRAMID

Meek & Worthen (1868*a*, p. 357; 1873, p. 514) state that the anal pyramid in *Lepidodiscus squamosus*, which they refer to as the "ovarian ? pyramid," is "closed by ten pieces, apparently imbricating laterally, and forming a depressed cone."

There are more than ten plates in the anal pyramid, and they are not arranged in the regularity shown in Meek & Worthen's figure. In addition to a few very small plates at the periphery of the pyramid, which are inserted between the outer edges of the large plates, there appear to be 15 plates in the anal pyramid of the holotype (pl. 120, fig. 3; text-fig. 1). Of these, only 11 extend into the central part of the pyramid. It is not known whether the number, size, shape, and arrangement of the plates vary within the species.

PERIPHERAL PLATES

Clarke (1901, p. 193) considered the nature of peripheral plates to be an important generic character, together with the nature of the interambulacrals and the length and width of the ambulacra. He diagnosed *Lepidodiscus* (in which he included *L. squamosus* and *L. alleganius*, the latter subsequently made the type species of *Cooperidiscus* by Bassler in 1936) as having "peripheral band very narrow or extinguished, composed of large and small plates; the latter few, the former projecting on the aboral surface." He contrasted it with *Agelacrinites*, in which the "peripheral band [is] composed of large plates with very small ones at the margin," and with *Discocystis*, in which the "peripheral band [is] composed of a few large plates with no fine ones outside of them."

Other workers have paid little attention to the peripheral plates in classification of edrioasteroids. They have regarded the nature of the covering plates of the peristome, the curvature of the ambulacra, and the interambulacral plates as diagnostic.

In contrast to other species assigned to *Lepidodiscus*, the type species does not have the peripheral plates fused to form a ring.

The plates lying outside the distal parts of the ambulacra are set at a steep angle, nearly vertical. The peripheral plates are very large, with the exception of the outermost plates, which are small and arranged in several rows. In the holotype the small plates are worn and, where preserved, more or less hidden by over-hanging adjacent large plates. In the left posterior region of the holotype, where the distal parts of ambulacra I, II, and III have been displaced over the edge of the peripheral plates, the latter are hidden in an oral view and are turned outward and upward toward the edges of the abulacra.

PERISTOMIAL REGION

The covering plates of the peristome appear to be smaller than those of the ambulacra. It is possible, however, that some of the plates are cracked and that some of the cracks have been interpreted as junctions between plates.

The center line of ambulacrum III continues into the peristomial region as a serrate line, and from its end one serrate line extends to the left to the junction of the center lines of ambulacra I and II, and another extends to the right to the junction of the center lines of ambulacra IV and V. Dr. August Foerste noted this arrangement in many edrioasteroids of the family Agelacrinitidae and (1914, p. 412) proposed a trimerous origin of the ambulacral system in the family. *Lepidodiscus squamosus* is an excellent example of a trimerous arrangement and "pseudo-pentamerism," as termed by Dr. Foerste. Some of the covering plates along the three lines have serrate edges. As already pointed out, this is a sharp contrast to the ambulacral covering plates, which are so arranged that the plates meet the central zigzag line without indentations.

The peristomial region (pl. 119, fig. 2; text-fig. 1) is strongly asymmetrical. The left half is very narrow, about the same width as the proximal part of one of the ambulacra. The right half, however, has a doubly lobate bulge projecting into the posterior ambulacrum. Many of the plates along a line parallel to the edge of this bulge are crushed in, suggesting that some hollow structure existed in the edrioasteroid below the covering plates. A similar structure has been reported in *Lepidodiscus ephraemovianus* (Bogolubov) by Hecker (1940, p. 99; 1941, p. 321) and pointed out again by Regnéll (1950, p. 5), who referred to it as "a bulging into the anal interambulacrum of the oral field suggesting the presence of some wider opening, according to the interpretation of Hecker."

The presence of a hydropore in edrioasteroids was first reported by F. A. Bather in 1900, in Part III of *A Treatise on Zoology*, edited by E. Ray Lankester. In his description of the class Edrioasteroidea, Bather wrote (1900*a*, p. 205), "Hydropore (usually, if not always, present) between mouth and anus." In Fig. VI, no. 1, he illustrated *Ediroaster bigsbyi* in a drawing, in which the hydropore was labeled "M" and identified in the explanation of the figure as a "madreporite." Because *A Treatise on Zoology* became a widely quoted text, many subsequent writers on the Edrioasteriodea have stated that edrioasteroids are characterized by a hydropore. Although this may be true, the existence of a distinct opening that can be interpreted as a hydropore has only been established in the genus *Edrioaster*.

In the same year that Part III of the *Treatise* was issued (but later, since it contains a reference to the *Treatise*), Bather published an article on "*Edrioaster Buchianus* Forbes sp.," in which he states (1900*b*, p. 198), "In the posterior interradius was a madreporite or hydropore-plate, the inner surface of which formed a semicircular projection for the attachment of the upper end of the stone-canal." Later Bather (1914*a*, p. 118) republished his figure of *Edrioaster bigsbyi* from Lankester's *Treatise* but labeled the structure "water-pore," and stated on the same page, "In the posterior interradius, two large interradials, adjoining the peristome, are traversed by an elongate hydropore." Evidently, Bather considered "hydropore," "madreporite," and "waterpore" to be synonyms.

Bather (1915*b*, p. 266) states that in the Agelacrinitidae "An external hydropore has not yet been detected, but it is conceivable that the hydrocircus [ring canal] opened into the oral vestibule, and that it may have been connnected with some canal passing up in the posterior interradius."

Edrioasteroids so preserved that the peristomial cavity can be viewed from the aboral side are extremely rare. Some specimens of

Carneyella pileus (Hall) in this condition have been studied by Foerste (1914, p. 427–429). He reports and figures (1914, p. 429; pl. 1, fig. 5*a*; pl. 2, figs. 3–4) "a peculiar margined depression along the proximal part of the right hand margin of the right posterior ray (No. 5), as viewed from below," and states, "This impression involves the two proximal covering plates on the left side of the right posterior ray, where adjoining the right margin of the posterior peristomial plate, as seen from above. Possibly a duct passed by this path, but its presence could not be verified with confidence."

Bather (1915*b*, p. 266) concluded, "If, as Dr. Foerste suggests, 'a duct passed by this path,' then the duct in question would most naturally be the hydropore-canal."

Foerste's description further indicates the possibility that the hydropore in *C. pileus* may have been an elongate slit between plates in the right posterior part of the peristomial region. Of these plates, he says (1914, p. 415):

> This differentiation [in form of the first covering plate of ambulacrum V] is connected with the form of the posterior peristomial plate, and consists in a slight elevation of the basal margin of the covering plate, corresponding to a much more marked raising of the lower right-hand margin of the posterior peristomial plate (P). Usually the first covering plate of the right posterior ray (No. 5) fits snugly against the upper part of the right hand margin of the posterior peristomial plate, often having a convex outline where adjoining the latter, but posteriorly these two plates do not fit as closely to the anterior outline of the immediately adjacent interambulacral plate (X). This suggests the possibility of the exit of some duct at the angle between these three plates (P, X, and 5). No aperture actually penetrating a plate has been noted.

As shown in one of Foerste's figures of *Carneyella pileus* (1914, pl. 1, fig. 5*a*), his plate "X" seems to be part of the peristomial region, since it lies wholly within the boundary formed by a continuation of the line along the rear edge of the posterior peristomial plate to the rear edge of the first covering plate of ambulacrum V.

Although *Carneyella* belongs to the family Hemicystitidae, it is of particular interest that a structure resembling a passageway for a stone canal is present in the peristomial region and that the form of the plates overlying it suggests an opening between them. The cavity in *C. pileus* lies below the plates in the right posterior part of the peristomial region which are not paired by plates on the left; thus, the cavity is covered by plates which enlarge the right posterior area and cause the peristomial region to be asymmetrical.

It may likewise be said of *Lepidodiscus squamosus* that the additional plates in the right posterior part make the peristomial region asymmetrical. The crushing in of the plates in this part strongly suggests that this unpaired structure was underlain by a hollow duct. No opening that could be termed a distinct hydropore was observed, although the plates are caved in and distorted so that even a large hydropore might not have been preserved.

Such an important part of the edrioasteroid's anatomy as the water-vascular system must have existed in all species. The distinct opening in *Edrioaster bigsbyi* is, in our opinion, rightly interpreted as a hydropore. We believe that the water-vascular system of other edrioasteroids also had some sort of opening for intake of water.

If numerous edrioasteriods could be obtained in each species, one might learn more about their internal structures by serial sections. Unfortunately, only one specimen of *Lepidodiscus squamosus* is known.

The evidence and observations just mentioned are meagre and inconclusive. We can only postulate the following:

1. Each edrioasteroid had some kind of water-vascular system, with an external opening, or hydropore, for intake of water.
2. In *Edrioaster* (family Edrioasteridae) the conspicuous opening shared by two adjacent plates in the posterior ambulacrum, near the right posterior edge of the peristomial region, is a hydropore.
3. In *Carneyella* (family Hemicystitidae) the hydropore is an inconspicuous gap between covering plates in the right posterior part of the peristomial region.
4. In *Lepidodiscus* (family Agelacrinitidae) the hydropore is probably a narrow gap between covering plates in the right posterior part of the peristomial region.

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JOURNAL OF PALEONTOLOGY, V. 32, NO. 5, P. 933–936, PL. 121, 1 TEXT-FIG., SEPTEMBER 1958

TIMEISCHYTES, A NEW GENUS OF HEMICYSTITID EDRIOASTEROID FROM THE MIDDLE DEVONIAN FOUR MILE DAM LIMESTONE OF MICHIGAN

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ABSTRACT—A very small and unusual edrioasteroid from the Dock Street clay member of the Four Mile Dam limestone (Middle Devonian) is classified as a new genus and species, *Timeischytes megapinacotus*. Although it appears to be closely related to *Hemicystites*, its inclusion in the Hemicystitidae requires an emendation of the family. The new species has two features unknown in other edrioasteroids. The anal pyramid is very large and touches the peristomial region, and each interambulacrum, with the exception of the posterior, is covered by one large plate.

INTRODUCTION

IN 1955, while cleaning some invertebrates from the Dock Street clay member of the Four Mile Dam limestone, the senior author noticed a small edrioasteriod attached to a bryozoan colony encrusting a coral. In 1958 in the course of investigating the edrioasteroid fauna of the Middle Devonian rocks of Michigan, we examined this specimen in detail. Preliminary cleaning revealed some very unusual characteristics.

A search was started for additional specimens in the collections of the Museum of Paleontology. Each of hundreds of fossils from this member was examined with a hand lens. The efforts were rewarded. Mr. Rex M. Peterson, an assistant at the Museum, found a second specimen. Curiously, this specimen, like the first, is attached to a bryozoan colony encrusting a coral. The label accompanying the second specimen indicates that it was found by Mr. Leon O. Pettyes, of Alpena, Michigan, who presented several invertebrates to the Museum of Paleontology on August 24, 1926. Evidently, the edrioasteroid had not been noticed until our search was made.

The first specimen, which we have designated as the holotype, is from an exposure of the Dock Street clay member of the Four Mile Dam limestone in the abandoned quarry of the Thunder Bay Quarries Company, now owned by the Huron Portland Cement Company of Alpena. This quarry is on the eastern side of Alpena, Michigan, in the SE ¼ sec. 14, T. 31 N., R. 8 E. The type section of the Dock Street clay member is exposed in this quarry, and is not known in other outcrops. Undoubtedly, the second specimen was also obtained from this locality.

The two specimens are catalogued and deposited in the Museum of Paleontology of the University of Michigan.

SYSTEMATIC DESCRIPTION

Phylum ECHINODERMA
Class EDRIOASTEROIDEA Billings, 1858
Family HEMICYSTITIDAE Bassler, 1936

Although the new edrioasteriod described in this paper appears to be closely related to *Hemicystites* Hall, particularly in the arrangement of plates in the peristomial region, its inclusion in the Hemicystitidae requires an emendation in the family description.

Bassler (1936, p. 4) originally described the Hemicystitidae as follows: "Theca composed of thin plates with an oral surface of five ambulacra separated by interambulacrals and attached by the greater part of the aboral surface permanently or temporarily to some outside object. Oral covering plates three, one large plate next to the anal area with two smaller adjacent ones."

He also characterized the Agelacrinitidae (1936, p. 15) as having a "theca as in the Hemicystitidae except that the plates covering the oral area are small, numerous, and without any definite order."

According to our analysis, the peristome in *Hemicystites* and related genera now included in the Hemicystitidae is covered by four plates. In addition to the three mentioned by Dr. Bassler, they include a fourth in the right posterior region. This plate was

described and figured in *Carneyella pileus* by Dr. Foerste (1914, p. 429; pl. 1, fig. 5a), who referred to it as plate "X" and classified it as part of the posterior interambulacrum. Foerste's account of this plate is quoted in the previous article under the center heading of "Peristomial region."

The new edrioasteriod has more than four plates covering the peristome. Unlike the Agelacrinitidae, however, it has the covering plates arranged in a definite pattern. The plate corresponding to Foerste's plate "X" in *Carneyella pileus* is large, conspicuous,and seems to be a definite part of the peristomial region.

To accommodate the new genus, we believe the description of the family Hemicystitidae should be emended to read as follows:

> Attached edrioasteroids with sacklike, cylindrical, or discoidal thecae composed of distinct plates. Peristome covered by four or more plates, of which four have a definite arrangement. Three meet in the center of the peristomial region; of these, one lies over the posterocentral part of the peristome, and the other two in the left anterior and right anterior positions, one on each side of ambulacrum III. The fourth, unpaired, lies in the right posterior part of the peristomial region. Proximally, ambulacrum V is constricted where it extends along the right side of this plate. Floor plates of ambulacra uniserial.

TIMEISCHYTES, n. gen.

Type species.—Timeischytes megapinacotus, n. sp.

Description.—Attached, discoidal. Ambulacra short, straight, broad. Ambulacra I and II joined together at the left side of the peristomial region, and ambulacra IV and V at the right side. Peristome covered by more than four plates. Posterior half of peristome covered by several plates, of which one is central and the unpaired plate lies in the right posterior corner. Ambulacrum V extending along the right edge of the latter, not symmetrical to ambulacrum I. Interambulacra with very few plates. Peripheral ring large, shaped like the frustrum of a cone, composed of a few large, thick plates with numerous small, scalelike plates on their distal surfaces and edges.

Remarks.—The new genus is very similar to *Hemicystites*, from which it differs in having several plates in the posterior half of the peristomial region instead of only two. It also has fewer interambulacral plates.

We have not considered the size of the anal pyramid, the number of plates in the anal pyramid, the exact number of plates in the interambulacra, nor the small size of the new edrioasterioid to be generically significant.

The name of this genus is an anagram of *Hemicystites*, a genus which it closely resembles; it is also based on the Greek τιμηεις ("precious, prized, costly"), in view of the efforts expended in finding the paratype, and χυτος, m. ("a mound"), referring to its shape.

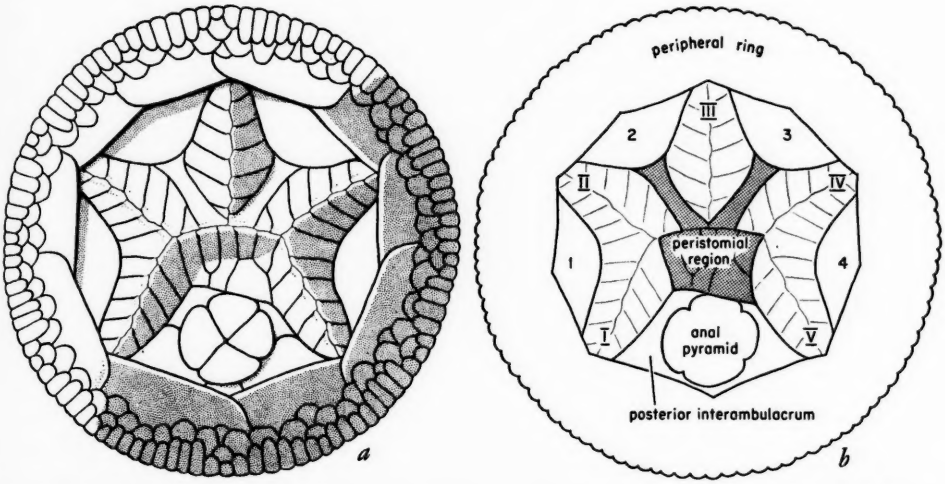
TIMEISCHYTES MEGAPINACOTUS, n. sp.
Pl. 121, figs. 1–6; text-fig. 1

Theca.—Very small, discoidal, attached. Peripheral ring wide. Ambulacra and peristomial region very large in relation to the interambulacra, together forming a modified, dilated pentacle within the peripheral ring. Anal pyramid large. Plates of the theca slightly granular, none highly ornamented but a few faint ridges on some interambulacrals.

Ambulacra.—Each ambulacrum short, straight, very broad proximally, tapering rather abruptly. Distal end subround, tangent to the peripheral ring or extending a little way under its edge. Ambulacra not sharply differentiated from the peristomial region. Ambulacrum I confluent with II, and ambulacrum IV with V. Center lines of I and II joined to the left end of the transverse center line of the broad peristomial region; these of IV and V joined to the right end. Center line of III extending posteriorly a short distance to the center of the peristomial region.

Ambulacral covering plates arched or vaulted upward toward the center line of the ambulacrum at an angle of about 30 degrees. Upper edges of plates turned slightly upward and beveled to form a narrow, more or less flat surface along each side of the center line.

Each ambulacrum covered by four or five plates on one side more or less alternating with four or five on the other side. Each covering plate subquadrate, with the following exceptions: on the anterior sides of II and IV, the proximal plate subtriangular and much smaller than the adjacent plate; the two posterior plates of III very small, subtriangular; the plate shared by I and II and the similar plate shared by IV



TEXT-FIG. *1—Timeischytes megapinacotus*, n. sp. *a*, reconstruction in oral view, based on the holotype and paratype; The proximal plates of ambulacra II–IV are drawn to agree with those of the holotype. *b*, labeled diagram of parts of the theca. The left posterior, left anterior, right anterior, and right posterior interambulacra are designated 1–4. The left posterior, left, anterior, right, and right posterior ambulacra are designated I–V, in accordance with common practise of numbering the ambulacra in a clockwise (solar) direction around the posterior interambulacrum.

and V large, subquadrate except for their acuminate inner ends; and terminal plates in each ambulacrum subtriangular. The proximal plate on the right side of I extending to the posterior interambulacrum, its right edge terminating anteriorly at the junction of the center lines of I and II. On the anterior sides of II and IV, the proximal one or two plates truncated by the peristomial region, not extending to the interambulacrum. On each side of III, the proximal one or two plates similarly truncated by the peristomial region (text-fig. 1). The proximal plate on the left side of V abutting against the right posterior (unpaired) peristome covering plate, not in contact with the posterior interambulacrum.

Interambulacra.—Interambulacra 1–4 each covered by one large sublunate or sublinguiform plate. Proximally, the plates of interambulacra 2 and 3 with a slightly smaller radius of curvature than those of 1 and 4 (pl. 121, fig. 5).

Posterior interambulacrum about half covered by the circular anal pyramid. Five plates around the anal pyramid (pl. 121, fig. 5): a small subtriangular plate at the right anterior side of the pyramid; a slightly larger plate at the left anterior; two large, subtrapezoidal, anteriorly acuminate plates, one at the left posterior and the other at the right posterior side; and a small subquadrate, narrow plate at the posterior.

Peristomial region.—Region broad, large, not distinctly differentiated from the ambulacra, divided into anterior and posterior parts by a long transverse center line extending from the junction of the center lines of ambulacra I and II at its left end to that of the center lines of IV and V at its right end. The two limbs of this transverse line forming an angle of about 160 degrees. Center line from ambulacrum III extending a short distance posteriorly to its junction with the center of the transverse line, forming an angle of about 100 degrees with each of its limbs.

Anterior part of the peristome covered by two large, elongate, subpentagonal plates, one situated on each side of ambulacrum III in an interambulacral postion. Each of these plates with its posterior side along the transverse center line, its two long, slanting sides nearly parallel, and its distal side abutting against the large interambulacral plate. The juncture of the two plates in this part of the peristome very short, along the extension of the center line of ambulacrum III.

Posterior part of the peristome asymmetrical, covered by six plates. Of these, only three extend to the posterior interambu-

lacrum. Plate over the posterocentral part of the peristome elongate, its anterior end abutting against the middle of the transverse center line and in contact with both anterior convering plates of the peristome; posterior half of this plate offset slightly toward the left. To the left of this plate, a smaller subtriangular to spatulate plate in contact with the transverse center line but not extending to the posterior interambulacrum. Between this plate and the proximal covering plate of ambulacrum I, an elongate subpentagonal plate in contact anteriorly with the transverse line and posteriorly with the interambulacrum; the posterior part of this plate in contact with the posterocentral covering plate of the peristome. The unpaired right posterior covering plate very large, subtrapezoidal, the only peristome covering plate not in contact with the transverse center line; its posterior border very long adjacent to the anal pyramid, its left border adjacent to the posterocentral covering plate, its anterior border in contact with a small plate of the peristome, and its right border in contact with three plates, one of the peristome and two of ambulacrum V. The other two plates of the region small, subquadrate, located to the right of the posterocentral plate and in front of the large unpaired plate.

Anal pyramid.—Very large, subcircular, quatrefoliated, in contact with the unpaired plate of the peristome. The four plates about equal, meeting in the center of the pyramid, their junctures forming an ×.

Peripheral ring.—Wide, shaped like the frustrum of a cone, its sides set at angles of about 35 degrees. Composed of about ten large, thick plates, slightly overlapping at their junctions but forming a rigid structure, and numerous smaller, thin plates on their distal surfaces and edges. Where smaller plates are missing, the large plates can be seen to extend to or nearly to the base of the theca.

Dimensions.—Holotype about 4.5 mm. in diameter; paratype about 4 mm.

Remarks.—The only two specimens that have been found are each attached to bryozoa that are encrusting a coral, *Depasophyllum adnetum* Grabau. This occurrence suggests that the larval edrioasteroids may have selected corals for attachment in order that they might avoid the accumulation of sediment, toxicity from decaying matter, or competition for food on the sea floor. The porous and uneven surface of the bryozoan colony may have offered favorable conditions for attachment to the larval edrioasteroid.

This edrioasteriod is unique in having the anal pyramid in contact with the peristomial region and in having four of the interambulacra each covered by a single plate.

We have considered the possibility that these specimens are immature, and that the adults may have differed in some characteristics. However, the plates in the specimens are well formed, with distinct boundaries and junctions, very unlike the plates in immature edrioasteroids we have studied. We believe, despite their very small size, that the edrioasteroids described above are fully developed adults.

The trivial name of the species is derived from Greek *μεγας* ("large, great") and *πιναξ*, m. ("plate, platter"), and refers to the form of the interambulacral plates.

Types.—Holotype, UMMP No. 35392. Paratype, UMMP No. 35428.

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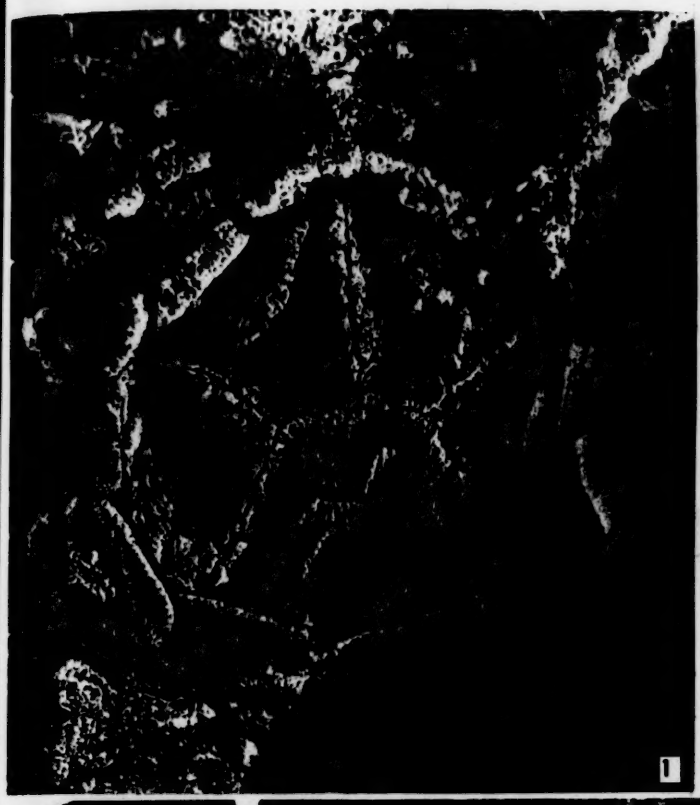
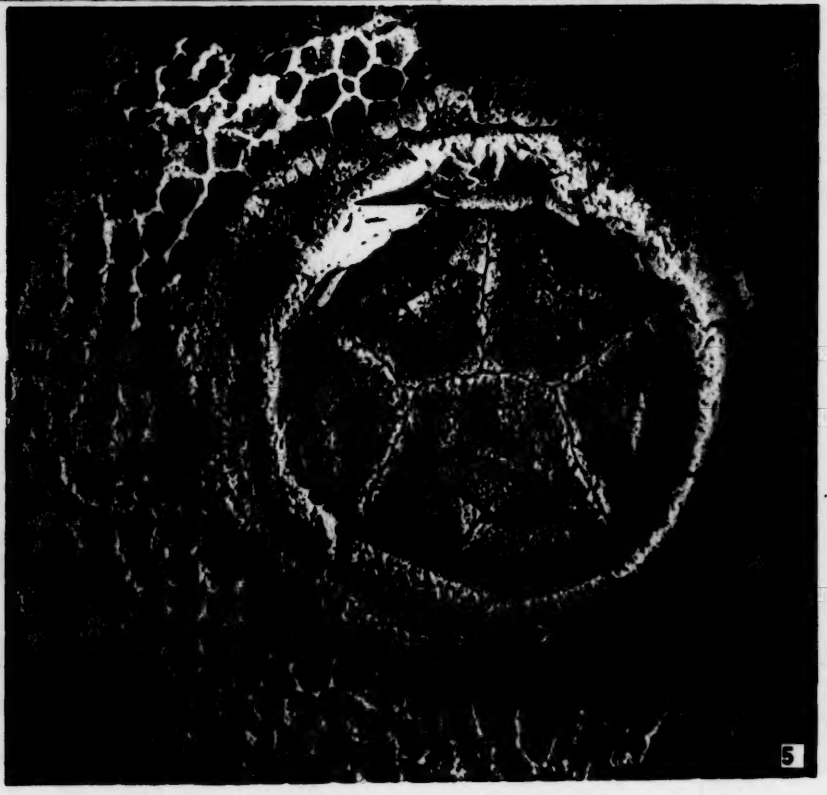
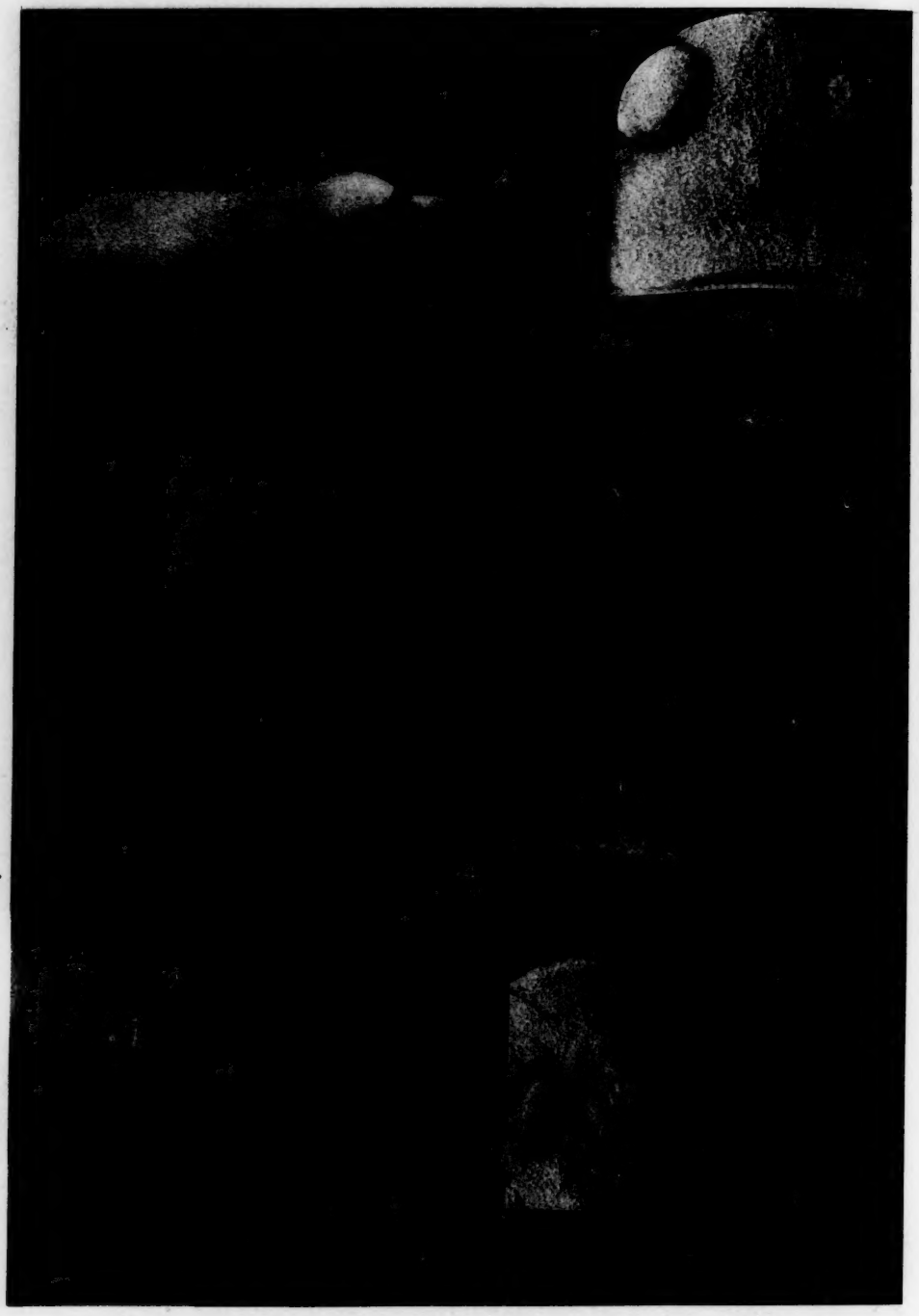
EXPLANATION OF PLATE 121

FIGS. *1–6—Timeischytes megapinacotus*, n. sp. *1–3*, holotype, UMMP No. 35392; the left side of the specimen, including interambulacrum 1 and parts of ambulacra I and II, were covered by matrix; when this matrix was removed, the plates were plainly visible when the specimen was wet, but are obscured by the very thin coating of sublimate used for the photographs. *1*, oral view, ×20; *2*, inclined posterior view, ×10; and *3*, inclined right view, ×10. *4–6*, paratype, UMMP No. 35428, an excellent specimen but with the proximal edge of the peripheral ring broken in the anterior region. *4*, oral view of the specimen (in the left central part of the picture, above the arrow) attached to a bryozoan colony encrusting a coral, *Depasophyllum adnetum* Grabau, ×1; *5*, oral view, ×20; and *6*, inclined left view, ×12¾.







JOURNAL OF PALEONTOLOGY, V. 32, NO. 5, P. 937–942, PL. 122, SEPTEMBER 1958

EURYPTERIDS FROM THE SILURIAN TYMOCHTEE DOLOMITE OF OHIO

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ABSTRACT—*Pterygotus* (*Acutiramus*) *perryensis* and *Eurypterus ornatus*, new species of eurypterids, are reported from the sparsely fossiliferous Tymochtee (Upper Silurian) dolomite of Fayette County, Ohio. A trail terminating in possible eurypterid remains is also described from the Tymochtee dolomite.

INTRODUCTION

THE Bass Islands group constitutes the youngest Silurian rocks in Ohio. In the northern part of the state, four formations are distinguishable. These are, in ascending order, the Greenfield, Tymochtee, Put-in-Bay and Raisin River dolomites. Carman (1927) correlated the group with outcrops in southern Ohio. The Raisin River and Put-in-Bay dolomites have not been definitely recognized here. They were evidently removed by Paleozoic erosion, which bevelled or totally stripped underlying units farther south. In the southern outcrop area, with which we are concerned, there are scattered exposures of the Tymochtee dolomite in Fayette, Ross, Highland, Pike, and Adams Counties.

The Tymochtee dolomite is inferred to be about 150 feet thick, but nowhere is the entire formation exposed. Few fossils have been reported from this unit. Carman (1927, p. 490) stated:

> The fauna . . . is a very meager one in number of species and individuals. The two most usual fossils are a small *Hindella* and a small *Leperditia* which cannot be distinguished from *Hindella rostralis* and *Leperditia ohioensis* of the Greenfield except by their smaller size. The fauna is not distinct from that of the Greenfield and contains only a few depauperate forms which were able to live on in spite of the adverse conditions.

Grabau & Sherzer (1910, p. 33) indicated the presence of *Leperditia alta* and a possible *Modiolopsis* in northern Ohio at the type section of the Tymochtee. In addition to *Leperditia* and *Hindella*, Miller (1955, p. 72) found *Hexameroceras*, *Michelinoceras?*, probable stromatoporoids, and unidentified high-spired gastropods in this formation in southern Ohio. The present writer has also collected winged pelecypods provisionally identified as *Pterinea*.

During 1957, Prof. J. E. Carman showed the author a previously undescribed *Pterygotus* from the Tymochtee dolomite. This specimen prompted a visit to the locality from which it had come, and to a few adjacent outcrops. *Eurypterus ornatus* was discovered at that time. A third specimen in the Ohio State University Museum was called to my attention by Dr. M. F. Marple. Eurypterids evolved rapidly, and were very abundant locally. Consequently, they are excellent stratigraphic indicators. It is earnestly hoped that more of these interesting arthropods will be found in southern Ohio.

The first two specimens described are preserved in crystalline dolomite, which re-

EXPLANATION OF PLATE 122

All specimens on this plate are from the Tymochtee dolomite of Ohio. Figures are retouched photographs.

FIGS. *1–3*—*Pterygotus perryensis*, n. sp. Anterior, lateral, and dorsal views of the holotype, O.S.U. No. 22049. *1*, *2*, ×1.5; *3*, ×1.

4,5—*Eurypterus ornatus*, n. sp. *4*, dorsal view of the holotype, a concave external mold; *5*, portion of a latex cast made from the holotype showing relief of the pustules, O.S.U. No. 22050. *4*, ×1.5; *5*, ×1.2.

6—Eurypterid? Prosoma and trail, ×2. O.S.U. No. 20561.

tains the original shape of the animal. It is striking that Silurian eurypterids are relatively uncommon in carbonates other than dolomite, either finely crystalline or argillaceous "waterlimes" and "platten dolomites." Unless these strata represent primary dolomite or penecontemporaneously altered limestones, as some have argued from the close association of these lithologies with evaporites, it is strange that eurypterids are rare in limestones or shaly limestone (cf. Størmer, 1934, p. 67–69; Brooks, 1957, p. 896). The eurypterids found in crystalline dolomites normally are little crushed or distorted while those obtained from the more argillaceous sediments are almost invariably flattened (cf. Clarke & Ruedemann, 1912, p. 180).

ACKNOWLEDGMENTS

The writer wishes to thank Prof. J. E. Carman, Ohio State University, for calling to his attention the *Pterygotus* described here, and for helping him to locate Upper Silurian exposures in southern Ohio. Erik N. Kjellesvig-Waering kindly criticized the manuscript of the paper and offered helpful suggestions on the taxonomic affinities of these eurypterids.

SYSTEMATIC DESCRIPTIONS

Subclass EURYPTERIDA Burmesiter 1843
Superfamily EURYPTERACEA Burmeister 1845
Family PTERYGOTIDAE Clarke & Ruedemann 1912
Genus PTERYGOTUS Agassiz 1839
Subgenus PTERYGOTUS (ACUTIRAMUS) Ruedemann 1935

PTERYGOTUS (ACUTIRAMUS) PERRYENSIS, n. sp.

Pl. 122, figs. 1,2,3

Description.—The holotype is a mold and cast of the prosoma preserved in finely crystalline dolomite. The specimen has a maximum width of 45 mm. along the base and a length of 35 mm. The prosoma is subrectangular in plan, with a "U" shaped anterior and an almost straight base. It is moderately convex, and the compound eyes protrude well above the prosomal surface in such a way as to suggest that there has been little crushing from the original convexity. The anterior margin is very gently rounded to the forward ends of the compound eyes. The radius of curvature then increases gradually to form the smoothly rounded antelateral angles. From the posterior ends of the eyes to the postlateral corners, the lateral margins are straight. They diverge posteriorly only 3 mm. in a distance of 14 mm. The posterior margin is slightly concave. A chord of this arc (45 mm. long) has a rise of only 3 mm. The sharp genal angles are only slightly less than 90°. The lateral edges are strongly incurved. The outer edges, although gently arched, are not bent. The central portion of the shield is almost flat.

The compound eyes are large and protruberant. In plan, they are symmetrical ovals with a major diameter of 14 mm. and a minor diameter of 10 mm. They have a depth of 4.5 mm. at the anterior margin. At their inward and inner posterior edges, they are smoothly streamlined into the dorsal shield. The eyes converge anteriorly, their long axes being 20 mm. apart at the anterior ends and 37 mm. apart at the posterior.

The lateral margin is concealed next to the left eye. On the other side, it is well preserved and shows that the eye is actually intramarginal. The dorsal surface of the eye extends in a horizontal plane beyond the margin, then curves down and in to join the margin. The entire ovoid of the eye is tangent to the margin along part of its edge.

The surface of the eyes appears to be slightly rougher than the rest of the prosoma, and it may be that a vestige of the original facets is retained. The crystalline texture of the rock makes it impossible to ascertain this feature with certainty.

The ocellar mound is a low circular area 3 mm. in diameter. It is located 20 mm. from the anterior margin, 21 mm. from the lateral margins, and 14 mm. from the base. Ocelli are not distinguishable.

Occurrence.—Pterygotus perryensis was found by Prof. Carman on the dump of the Sugar Creek stone quarry, located on the south bank of Sugar Creek just west of State Route 70, 5.0 miles southeast of the town of Washington Court House, Perry Township, Fayette County, Ohio. The original label accompanying the specimen states that at the time it was found (1941), the only forma-

tion exposed in the quarry was the Tymochtee dolomite. Miller (1955, p. 178) indicated that subsequent quarrying operations exposed the top of the Greenfield dolomite at a depth of 80 feet 9 inches below the lip of the quarry.

Type.—Holotype prosoma in Ohio State University Museum, No. 22048 (cast), No. 22049 (mold).

Remarks.—The prosoma of *Pterygotus perryensis* differs from other American pterygotids in its great length to width ratio. The proportionately large eyes suggest that the specimen is an immature individual. If this is so, then by comparison of this characteristic with species such as *P.* (*Acutiramus*) *macrophthalmus* (Hall) and *P.* (*Acutiramus*) *cummingsi* Grote & Pitt, the mature animal might have had a length of more than 2.5 meters. The prominent ocellar mound is also suggestive of a young eurypterid. *P. perryensis* resembles *P. monroensis* Sarle, known from a single distorted prosoma found in the Pittsford shale of New York. The latter is distinguished by the peculiar angulation of the inner margins of the eyes. Clarke & Ruedemann (1912, p. 380, 381) noted that its eyes suggest *P. monroensis* may not be a *Pterygotus*.

Although species of *Pterygotus* have been recognized in formations ranging in age from Ordovician to Devonian, and in North America have been found at points as widely separated as Nova Scotia, Florida and Wyoming, this is the first specimen to be reported in the Bass Islands group, a unit long noted for eurypterids in northern Ohio [*Eurypterus eriensis* (Whitfield) from the Put-in-Bay dolomite].

No other fossils are associated on the slab with this specimen.

Family EURYPTERIDAE Burmeister 1845
Genus EURYPTERUS DeKay 1825
EURYPTERUS ORNATUS, n. sp.
Pl. 122, figs. 4,5

Description.—The species is based on a mold of the prosoma with the first tergite attached. This specimen, preserved in a slab of dense, very finely crystalline dolomite, shows not only the outline of the prosoma, but also its natural relief and ornamentation.

The length of prosoma, measured along the axis from the anterior to posterior margin, is 43 mm. Since the posterior margin is concave, the postlateral corners extend the length an additional 3 mm. The width at the base is 59 mm. Width at base of the eyes, 19 mm. forward from the posterior margin, is 57 mm. The width at the front of the eyes is 52 mm. In plan, the prosoma is subtrapezoidal. Posteriorly, the lateral margins are almost parallel, but converge increasingly as the antelateral angles are approached. The anterior margin is very gently convex, its arc being only slightly greater than the low arc of the base. Genal angles are sharp at approximately 90°.

A prominent marginal rim surrounds the shield on three sides. It is widest (2 mm.) at the middle of the anterior margin, slowly narrowing to 0.25 mm. at the postlateral angles.

The occipital furrow is first visible 9 mm. from the genal angles. It marks the margin of the smooth occipital band, which expands centrally to a maximum width of 2.5 mm.

Reniform eyes rise very slightly above the level of the center of the cephalothorax, but their surfaces curve precipitously downward on the outer and anterior sides, so as to stand fully 1 mm. above the adjacent prosomal surface. They are 8 mm. long, 20 mm. apart anteriorly, 22.5 mm. apart posteriorly and are located 13 mm. from the lateral margin at their outermost curvature, 14 mm. from the anterior margin. They appear to have given the animal an arc of vision of approximately 270°.

The prosoma bears a distinctive ornamentation of tiny raised pustules (see fig. 5, pl. 122). The surface of the occcipital band, the marginal rim, and arcuate areas about 2 mm. wide in front of and exterolaterally adjacent to each eye is smooth. At the inner edge of the marginal rim, there is another type of ornamentation: narrow pustules about four times as long as wide, the elongation paralleling the immediate margin. These scales become smaller but more elongate as the rim narrows. They accentuate the junction of the rim with the prosoma proper.

Precisely half way between the eyes and 19 mm. from the anterior margin is an ob-

scure, almost imperceptible, ocellar mound. The surface is poorly preserved, and no trace of the ocelli can be found.

The prosoma retains most, if not all, of its original convexity. The marginal rim slopes upward at an angle of about 30°. At the inner edge of the rim, the slope breaks abruptly to form a low, gradually flattening arch. The rectangular area, of which the posterior ends of the eyes constitute the anterior corners, is almost perfectly horizontal. Between the eyes and anterior to them, is a trapezoidal area, 18 mm. wide at the anterior ends of the eyes, and 13 mm. wide at the anterior margin. This area stands just high enough above the laterally adjacent surfaces to prevent the arc of vision of each eye from overlapping. Presumably it created a small triangular "blind spot" directly ahead of the animal.

The tergite is relatively straight, with a gently concave posterior margin which parallels the corresponding margin of the prosoma. This central concavity changes gradually to a convex curve, and in the last 10 mm. from either end, the posterior margin turns prominently and increasingly forward. Thus the tips of the segment are tapered to bluntly rounded points directed forward at an angle of about 30°. Greatest width of the tergite is 7 mm. and its maximum length is 61.5 mm. The left end of this segment shows small pustules similar to those which cover the prosoma, but ornamentation on the remainder of the surface is obliterated.

Occurrence.—The author found this specimen on a large slab of yellowish gray dolomite at the quarry dump of the Fayette Limestone Company. The location is the site of the former Walnut Hill School on the 1917 U. S. Geological Survey map of the Sabina, Ohio 15 minute quadrangle. This is 4.0 miles southwest of Washington Court House on U. S. Highway 62 in Green Township, Fayette County. According to Miller (1955, p. 180–182), the only formation exposed in this quarry is the Tymochtee dolomite. Marine fossils were observed at the site by both Miller and the present writer, but the eurypterid is not associated on the slab with any other fossils.

Type.—The holotype is a mold of the prosoma in the Ohio State University Museum, No. 22050.

Remarks.—*Eurypterus ornatus* shows a pattern of ornamentation quite distinct from that of any other North American *Eurypterus*. The ornamentation somewhat resembles that of the smaller *E. tetragonophthalmus* Fischer, of the Baltic Upper Silurian, but the prosomal length to width proportions clearly differentiate *E. ornatus* from this species. The length to width dimensions of *E. ornatus* (43:57) reduce to a ratio of 1:1.33. *E. tetragonophthalmus* has dimensions which reduce to approximately 1:1.44. From this, it is immediately apparent that *E. ornatus* possesses a much shorter, broader prosoma.

In addition, *E. tetragonophthalmus* has proportionately larger eyes. The length of the prosoma is a little more than 2.6 times the length of the eye, while in *E. ornatus*, the cephalothorax is over 5.3 times as long as the eye. Among other minor differences, the small pointed scales which ornament the posterior margins of the prosoma and segments in the Baltic species are absent.

In its outline and general proportions, *E. ornatus* is most comparable to *E. flintstonensis* Swartz. The latter is a Tonoloway species from western Maryland. The holotype of *E. flintstonensis* is also a cephalothorax with the first tergite attached. The length to width ratio of the prosoma is 1:1.50 and the ratio of the length of the eye to the total length is 1:3.00. These relationships show somewhat different proportions than those of *E. ornatus*, but a word of caution must be added here. The writer has carefully measured several dozen prosomas of *E. remipes* DeKay, the genotype. The result of this study has been to show that the length to width ratio changes during ontogeny. Specimens having a length of 10 mm. or less show an average ratio of about 1:1.39. Specimens over 20 mm. in length have a ratio of around 1:1.34. Thus any comparison of prosomal ratios must be referred to specimens of similar size. *E. flintstonensis* is based on a specimen only 12 mm. long. Judging from the rate of change observed in *E. remipes*, it seems that if a specimen of *E. ornatus* could be found which was no larger than the type of *E. flintstonensis*, there

would be no appreciable difference in the proportions.

It is well known that immature eurypterids have relatively larger eyes than adults of the same species, but the greatest change in proportions is restricted to the early growth stages (Clark & Ruedemann, 1912, p. 119). While it is possible that a smaller specimen of *E. ornatus* might have eye proportions more consistent with *E. flintstonensis*, the ratios seem too far apart to be explained in this manner (1:5.38 as against 1:3.00, respectively).

The chief distinction between the species is the lack of ornamentation in *E. flintstonensis*.

Class UNCERTAIN
Pl. 122, fig. 6

Description.—The Ohio State University Museum contains a very unusual specimen which is described here for the first time. The writer is unwilling to assign the fossil to the "catch all" genus, *Protichnites* Owen, which includes several types of trail markings, some possibly related to eurypterids (Sharpe, 1932). Moreover, this specimen is unique in that it consists not only of a trail, but at least a part of the organism which made the trail. The animal shows certain similarities to the Eurypterida, but does not closely resemble any known genus.

The specimen is preserved on an argillaceous bedding surface of a thin slab of gray dolomite. The fossil consists of a trail 20 mm. long and 10 mm. wide, with the remains of an animal at the end of the trail. Two rows of closely spaced, pointed, triangular impressions are 3 mm. apart. The surface between the tracks is slightly depressed, where the animal dragged its weight across the unconsolidated sediment. The tracks are flanked on each side by one third to one half as many slender, curved, shallow marks about 4 mm. long. It is impossible to count the exact number of steps, for none of the four rows is complete. They are terminated at one end by a break in the rock, and at the forward end, all of the marks are blurred.

At the end of the trail is an object which appears to be the cephalothorax of an arthropod. Its right side is poorly preserved, so that the description is based principally on the left half. The outline is subrectangular, 5 mm. long, 6 mm. wide at the base and 5(?) mm. wide at the eyes. The frontal margin is almost straight, curving into the bluntly rounded antelateral angles. The lateral margins meet the posterior margin at sharp right angles. The posterior margin is slightly convex. A prominent marginal rim is developed only along the anterior margin, and is widest at the center, where it measures about 0.5 mm.

A small rounded eye is present 2 mm. from the anterior and 0.5 mm. from the lateral margin. The eye is prominently raised, and is approximately 0.5 mm. in diameter.

The sides of the cephalothorax slope upward to a pronounced cardiac lobe which extends along the longitudinal axis for 2.5 mm. from the inner edge of the marginal rim. A transverse cross section of the prosoma would show a low triangle, its sides steeply concave as they approach an apex at the narrow cardiac lobe. Posterior to this lobe, the prosoma appears to have been almost flat, but the lobe's abrupt termination suggests that this portion may not have been preserved. Alternatively, the "cardiac lobe" may itself be adventitious, representing a fold formed by lateral compression of the right side of the prosoma.

Other faint marks on the surface of the slab cannot definitely be related to the fossil.

Occurrence.—The specimen was collected by Mr. Ralph Bernhagen, Ohio State Geologist, from the Tymochtee dolomite at the Ralph Rodgers Company Quarry. This is on an inlier of the formation along Sunfish Creek, 1.25 miles east of Byington, in Mifflin Township, Pike County, Ohio. Miller (1955, p. 157–158) indicated that only the lowest 20 feet of the Tymochtee dolomite is exposed in the quarry, and that not more than 40 feet of the unit is present in this area, where it is disconformably overlain by the Devonian Ohio shale.

Repository.—The Ohio State University Museum, No. 20561.

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CALYMENID TRILOBITES FROM THE ORDOVICIAN ROCKS OF MICHIGAN

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ABSTRACT—All known calymenid trilobites from the Ordovician rocks of Michigan are illustrated. Four new species and one new variety of *Flexicalymene* and one new species of *Papillicalymene* are described. The Middle and Upper Ordovician stratigraphy of the Northern Peninsula is briefly reviewed.

INTRODUCTION

THE RESULTS of a detailed morphological study of the Middle and Upper Ordovician calymenid trilobites of Michigan are presented in this paper. This study was initiated by the discovery of several previously undescribed species in the collections at the University of Michigan.

Collections examined in this study were obtained from localities in the Northern Peninsula of Michigan, where Middle and Upper Ordovician limestones and calcareous shales of Black River, Trenton and Richmond age form an arching east-west belt of rocks extending across the center of the peninsula. These sediments are well exposed at intervals along this belt, notably on Stonington Peninsula and in the valley of the Escanaba River (for index map of localities see Hussey, 1950, p. 30).

Additional specimens from well cores in southeastern Michigan and from outcrops of the Upper Ordovician of Ohio and the Middle Ordovician rocks in the vicinity of Trenton Falls, New York, were studied for comparison.

Specimens of *Flexicalymene senaria* (Conrad) illustrated by James Hall (1847), were examined, and, as the repository of Conrad's types is unknown, the original of Hall's pl. 64, figs. 3b–c is refigured as it is a characteristic and well preserved specimen.

Five new species and one variety are described, illustrated, and compared with *F. meeki* (Foerste), *F. meeki retrorsa* (Foerste), and Hall's hypotype of *F. senaria* (Conrad). Shirley's classification of the Calymenidae (1932, 1936) is reviewed and applied to the Michigan representatives of this family.

The stratigraphy of the Middle and Upper Ordovician of Michigan is briefly reviewed (see text-fig. 1) and the known stratigraphic ranges and occurrences of calymenid trilobites from these strata presented in text-figure 2.

ACKNOWLEDGMENTS

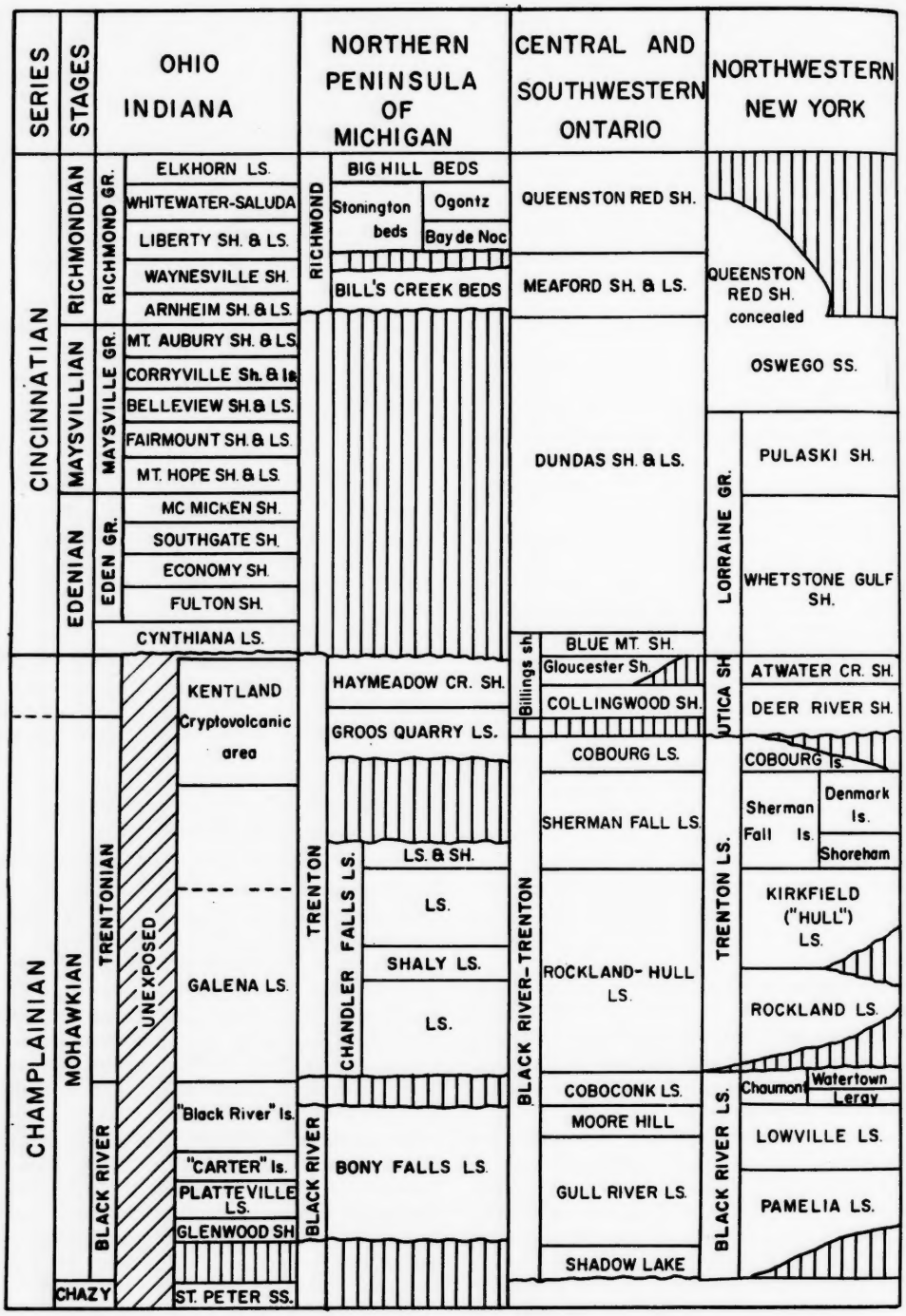
The authors wish to thank Dr. Russell C. Hussey of the Department of Geology, University of Michigan, for his kind assistance in this project. Dr. Robert V. Kesling of this university was also extremely helpful in many respects. A number of specimens were loaned for study by Dr. Hussey, Mr. Jackie Watkins, and Mr. Samuel Riggs. Dr. Donald Squires of the American Museum of Natural History loaned James Hall's original specimens of *Flexicalymene senaria*.

MIDDLE AND UPPER ORDOVICIAN STRATIGRAPHY OF MICHIGAN

Middle and Upper Ordovician strata in Michigan are represented by limestones and calcareous shales of Black River, Trenton, and Richmond age in the outcrop area in the Northern Peninsula. In addition, Chazyan sediments, represented by the St. Peter sandstone, have been discovered in well cores from southern Michigan, but are not exposed since they truncate against an upper Chazyan disconformity south of the outcrop belt.

In northern Michigan, Richmond strata rest unconformably on the Black River-Trenton sequence. Rocks of the Eden and Maysville groups, as well as the lower part of the Waynesville shale of the Richmond group, are not present in this area. They do outcrop, however, to the northeast on Manitoulin Island in Lake Huron.

In text-figure 1, Hussey's stratigraphic



TEXT-FIG. 1—Stratigraphic column of the Northern Peninsula of Michigan compared with those of Ohio-Indiana, Ontario, and northwestern New York.

SPECIES OF CALYMENIDAE IN MICHIGAN	MIDDLE ORDOVICIAN						UPPER ORDOVICIAN			
	BLACK RIVER		TRENTON			?	?	RICHMOND		
	S. MICH.	N. MICH.	S. MICH.	NORTHERN PENINSULA			NORTHERN PENINSULA			
	Undivided	Bony Falls m.	Undivided	Chandler Falls	Groos Quarry	Haymeadow Cr (Collingwood)	Bills Creek sh	Stonington beds: Bay de Noc	Stonington beds: Ogontz mbr.	Big Hill beds
F. senaria			X	X	X	X				
F. planilabra			X							
F. magnipapilla				X						
F. senaria parvicephala					X					
F. croneisi					X					
F. quadricapita							X			
F. praelongicephala							X			
P. husseyi									X	

TEXT-FIG. 2—Stratigraphic ranges of Calymenidae in Michigan (Note: *F. praelongicephala* from probable Bill's Creek shale equivalent at Limestone Mountain.)

divisions of the Middle and Upper Ordovician of northern Michigan are correlated with those of Ohio and Indiana, central and southwestern Ontario, and northwestern New York. Subdivisions below the formational level are indistinct in cores from the southeast part of the Michigan basin (Kauffman, 1956), where the formations are thicker and more uniform, and where paleontologic differentiation on this level becomes impractical due to overlapping ranges, or the absence of key index fossils used by Hussey and others.

The presence of disconformities and mixed index faunas in many of these beds has caused difficulty as well as a degree of uncertainty in the correlation of these units with those of areas where there is a better developed section, such as the Upper Ordovician of Ohio. Certain of these problems are worthy of note.

The Bony Falls member can be correlated only approximately with the upper Black River units of New York and Ontario, since several disconformable stratigraphic breaks, some representing a considerable length of time, occur in the section. In cores from the southeast Michigan basin, the Black River section is more complete, but has not been subdivided.

Although the Chandler Falls member is bounded above and below by disconformities, it possesses definite faunal associations with the Rockland-Hull and lower Sherman Falls formations, as well as having some Galena affinities. Thus, no real problem is encountered here. A basal conglomerate marks the beginning of this unit in some places.

The overlying Groos Quarry member is closely related to the Stewartville formation (upper Cobourg).

The biggest problem in correlation lies in the Haymeadow Creek-Bill's Creek shale sequence, which is exposed near the falls on Haymeadow Creek and in Bill's Creek, both in Delta County, Michigan. The two units, intermittently exposed along Bill's Creek, are very similar lithologically, and can be differentiated only by the slightly darker color of the underlying Haymeadow Creek shale and the characteristic light gray weathering surface and more even bedding of the Bill's Creek shale.

The Bill's Creek beds, sensu stricto, are correlated by Hussey with the Maquoketa and equivalent beds on the basis of the following forms collected from the northern Michigan sections: *Tetradella regularis*, an ostracod occurring in the basal Waynes-

ville shale (Richmond) of Ohio; *Primitia cincinnatiensis*, another ostracod from the basal Waynesville; *Bythopora striata*, a bryozoan found in the Arnheim formation and Waynesville of Ohio, Indiana and Kentucky; *Arthropora shafferi*, a bryozoan similar to one found in the lower Waynesville of Ohio; *Cleidophorus neglecta*, a pelecypod common in the basal Maquoketa formation in Iowa; and several species of *Lingula* common to the Maquoketa shales.

Since this publication, however, several of these faunal similarities have been questioned for one reason or another. For instance, the ostracod *Tetradella regularis* from the Waynesville shale is not the same as the ostracod of that same name from the Bill's Creek shale, and the latter has been subsequently redescribed by Kesling & Hussey (1953) and placed in their new genus, *Quadrijugator*, which is known only from the Bill's Creek beds. There is also some question as to the identification of *Primitia cincinnatiensis*. Further, many workers are inclined to be skeptical of any definite correlations based on species of *Lingula* until this group is more thoroughly studied.

It is evident, therefore, that the correlations are not as definite as they first appeared. The lower shaly unit, the Haymeadow Creek member, has faunal affinities with the Collingwood (uppermost Trenton?). This correlation is based largely on the pres-

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EXPLANATION OF PLATE 123

All figures ×2 unless otherwise noted

FIGS. *1–11—Flexicalymene senaria* (Conrad). *1*, anterior view of complete, unrolled specimen described by James Hall, 1847, pl. 64, figs. 3a–c. From the Hall collection at the American Museum of Natural History, no. 18431/1, Trenton Limestone, Watertown, New York. *2*, lateral view of same specimen. *3*, posterior view of same specimen, showing deeply grooved pleural segments of pygidium. *4*, ventral view of anterior border of same specimen, showing character of rostrum, rostral suture, and connective sutures. *5*, dorsal view of same specimen. *6*, cranidium lacking right fixed cheek. Hypotype No. 30065, Chandler Falls limestone, banks of Escanaba River, below power dam at Chandler Falls, Delta County, Michigan. *7*, cranidium lacking part of right fixed cheek. Hypotype No. 34225, horizon and locality, fig. 6. *8*, left fixed cheek and free cheek, showing nature of facial suture and ornamentation of preglabellar field. Hypotype No. 34227. Groos Quarry formation, Rapid River, east of bridge, station 13, just east of Rapid River, Delta County, Michigan. *9*, cephalon lacking right free cheek. Hypotype No. 34226. Collingwood shale, float blocks near Newberry, Michigan. *10*, cranidium with well preserved tuberculation lacking lateral parts of fixed cheeks. Hypotype No. 30068. Chandler Falls limestone, ledges along banks of Escanaba River below power dam at Chandler Falls, Delta County, Michigan. *11*, enlargement of part of median lobe, frontal lobe, and part of preglabellar field of fig. 10, showing openings in tubercles for sensory hairs. ×8.

12—Flexicalymene croneisi (Roy). Cranidium lacking right fixed cheek. Hypotype No. 34255. Groos Quarry limestone, in Escanaba River above the paper mill at Groos, Michigan.

13—Flexicalymene sp. cf. *F. senaria* (Conrad). Nearly complete cranidium, showing coarse tuberculation. Figured specimen No. 34256. Horizon and locality, fig. 12.

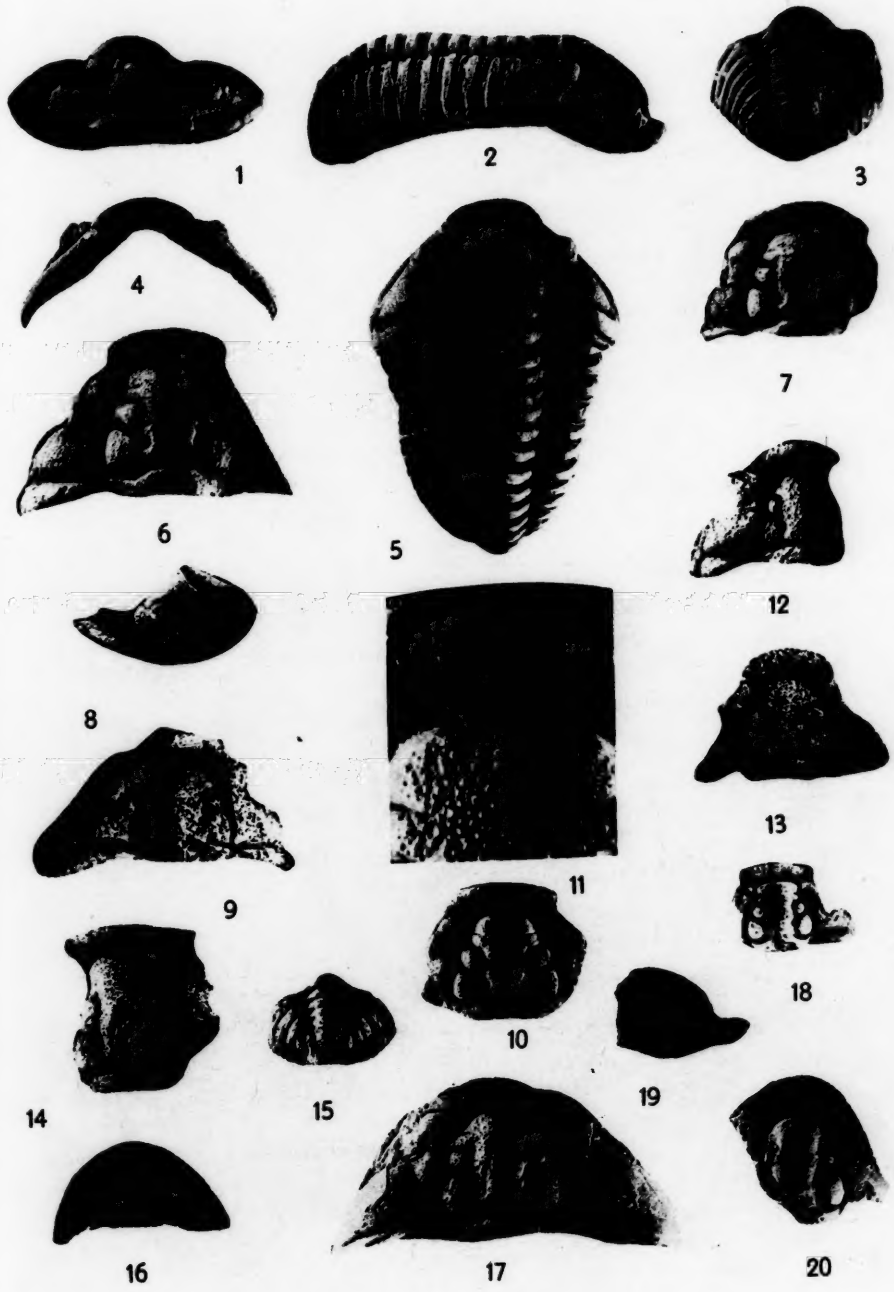
14–15—Flexicalymene praelongicephala, n. sp. *14*, cranidium lacking left fixed cheek and part of right fixed cheek. Holotype No. 34242. Lower Richmond (layer VI of Case and Robinson), Limestone Mountain, Houghton County, Michigan. *15*, complete pygidium with ungrooved pleural segments. Paratype No. 34243. Horizon and locality, fig. 14.

16—Flexicalymene senaria parvicephala, n. var. Complete cephalon. Holotype No. 34228. Groos Quarry formation, station 12 of Hussey, south side of island, in Escanaba River, just above paper mill at Groos, Michigan.

17—Flexicalymene magnipapilla, n. sp. Dorsal view of complete cephalon, showing coarse tuberculation of lateral glabellar lobes and occipital ring, nature of axial furrows. Holotype No. 30067. Chandler Falls limestone, ledges along banks of Escanaba River below power dam at Chandler Falls, Delta County, Michigan.

18—Papillicalymene husseyi, n. sp. Cranidium lacking part of left fixed cheek, showing well developed buttresses on fixed cheeks. Holotype No. 9905. Stonington beds, Ogontz member, east side of Little Bay de Noc, Michigan.

19–20—Flexicalymene planilabra, n. sp. *19*, right lateral view of cranidium, showing very convex, short glabella and fixed cheeks, nature of preglabellar field. Holotype No. 34244. Trenton formation, Buss-Halb unit no. 1 well core, Freedom Township, Washtenaw County, Michigan. *20*, dorsal view of same specimen, showing nature of antennary pits and node-like mediolateral glabellar lobe.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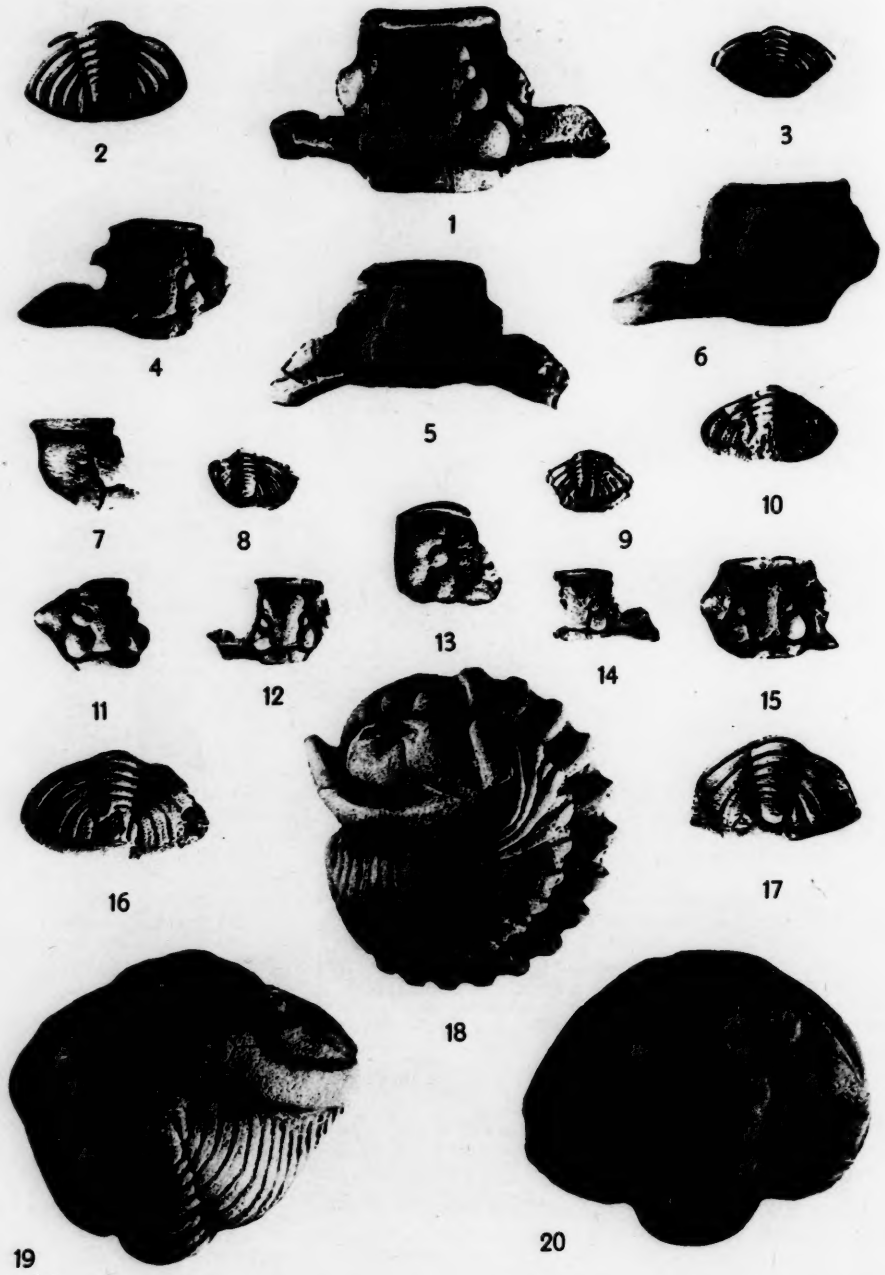
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ence of *Tetragraptus quadrimucronatus* in both formations.

If Hussey's correlations are correct, then a disconformity representing considerable time occurs somewhere in the shale section. As yet, this disconformity has not been discovered. In addition, the contact between the Groos Quarry member and the lower part of the Haymeadow Creek shale is covered. Hussey assumes that not much of the basal shale unit is missing and that since the dips of the two members are similar, the contact may well be a conformable one.

Hence, the actual age and affinities of the entire section between the Middle Ordovician Groos Quarry member and the Stonington beds of lower Richmond age, is still highly questionable.

At this time, the Bill's Creek shales have more known faunal affinities with the Richmond than with the upper Trenton, but more complete collections and additional detailed study are needed before any definite correlation can be made.

The typical Richmond sediments of the Northern Peninsula are more clear-cut in their correlations. The basal member of the Stonington beds, the Bay de Noc member, contains numerous fossils of Whitewater as well as uppermost Waynesville age, plus a few Elkhorn forms. The overlying Ogontz member is characterized by typical Whitewater forms. Thus, the lower part of the Bay de Noc has been correlated with the upper Waynesville and the upper part of the Bay de Boc and the Ogontz member with the Whitewater of Ohio. This correlation is tentative and based mainly on faunal associations. The Big Hill Beds, conformably overlying the Ogontz, are provisionally correlated with the uppermost Whitewater and Elkhorn formations of the Richmond group in Ohio.

OCCURRENCE OF CALYMENID TRILOBITES IN MICHIGAN

Calymenid trilobites, most of them belonging to the genus *Flexicalymene* Shirley (1936), have been reported from the Chandler Falls, Groos Quarry, and Collingwood

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EXPLANATION OF PLATE 124

(All figures ×2)

FIG. *1*—*Flexicalymene meeki retrorsa* (Foerste). Dorsal view of cranidium, showing sharply upturned preglabellar field and enlarged frontal lobe. Hypotype No. 34249. Richmond group, Waynesville formation, Blanchester member, Stony Hollow, one half mile northwest of Clarkesville, Ohio.

2–16—*Flexicalymene quadricapita*, n. sp. *2*, dorsal view of complete pygidium, showing moderately grooved pleural segments. Paratype No. 34257. Richmond group ?, Bill's Creek shale, near Ensign, Michigan. *3*, dorsal view of small complete pygidium. Paratype No. 9911. Richmond group ?, Bill's Creek shale, at Bill's Creek, Sec. 7, T. 41 N., R. 20 W., Delta County, Michigan. *4*, dorsal view of cranidium lacking part of right fixed cheek. Paratype No. 34258. Horizon and locality, fig. 2. *5*, complete cranidium showing quadrate frontal lobe, reduced anterolateral lobes, elongate posterolateral lobes, position of eyes and general nature of typical cephalon. Holotype No. 30066. Horizon and locality, fig. 3. *6*, dorsal view of cranidium lacking part of right fixed cheek, showing typical characteristics of species. Paratype 9917. Horizon and locality, fig. 3. *7*, right side of cranidium. Paratype No. 34259. Horizon and locality, fig. 2. *8*, dorsal view of incomplete pygidium. Paratype No. 34260. Horizon and locality, fig. 2. *9*, dorsal view of crushed pygidium. Paratype No. 34261. Horizon and locality, fig. 2. *10*, dorsal view of complete pygidium with weakly grooved pleural segments. Paratype No. 34262. Horizon and locality, fig. 2. *11*, glabella and part of left fixed cheek. Paratype No. 34263. Horizon and locality, fig. 2. *12*, partial cranidium, dorsal view. Paratype No. 34264. Horizon and locality, fig. 2. *13*, dorsal view of right side of cranidium, showing typical tuberculation. Paratype No. 34265. Horizon and locality, fig. 2. *14*, cranidium lacking left fixed cheek. Paratype No. 34266. Horizon and locality, fig. 2. *15*, dorsal view of incomplete cranidium. Paratype No. 34267. Horizon and locality, fig. 2. *16*, dorsal view of complete pygidium, with grooved pleural segments, Paratype No. 34268. Horizon and locality, fig. 2.

17—*Flexicalymene* sp. cf. *F. meeki* (Foerste). Dorsal view of complete pygidium. Figured specimen No. 34269. Horizon and locality, fig. 2.

18–20—*Flexicalymene meeki* (Foerste). *18*, left lateral view of complete enrolled specimen, typical of the species. Hypotype No. 34270. Richmond group, Lebanon, Ohio. *19*, anterior view of same specimen, showing non-grooved pleural segments of pygidium and character of doublure and hypostome. *20*, dorsal view of same specimen, showing rounded frontal lobe, position of eyes, and general character of cephalon.

members of the Trenton formation, and from the Bill's Creek beds of the Richmond group. In addition, a single specimen tentatively placed in Shirley's genus *Papillicalymene* is known from the Ogontz member of the Stonington beds. No calymenid trilobites have been reported from the Bay de Noc member or the Big Hill beds. Of special note is the absence of *Flexicalymene meeki* and *F. meeki retrorsa* in beds of Richmond age in Michigan. The only common calymenid trilobite in these beds is *F. quadricapita*, n. sp., from the upper Bill's Creek shale. A single pygidium similar to that of typical specimens of *F. meeki* has been found in the Bill's Creek beds near Ensign, Michigan.

F. quadricapita is radically different from *F. meeki* and related species in many respects, notably in the more posterior position of the eyes (opposite the mediolateral glabellar lobes in *F. quadricapita*, but opposite the anterolateral lobes in *F. meeki* and related species) and in the shape of the frontal lobe. The position of the eyes, according to Shirley (1936), may be of primary taxonomic importance, and in this respect he mentions *F. meeki*, *F. meeki retrorsa*, and related but less common species, as being a very close-knit group with the various species differing little from one another. It thus appears that the common lower Richmond form in Michigan is not only distinct from the *F. meeki* lineage, from equivalent beds in Ohio, but is not even closely related to it.

No definite explanation is possible for this phenomenon without a more complete study of the progression of flexicalymenid forms from beds in and around the Michigan Basin, although it appears that the distribution of these forms is a function of environmental factors for the most part. Perhaps the Michigan species is a boreal form, but the entire answer does not lie here, since *F. meeki* and related forms have been reported from equivalent latitudes in the same formations, presumably deposited in a continuous epicontinental sea.

Stratigraphic units from which calymenid trilobites have been collected are indicated in text-figure 2. More extensive collecting will obviously turn up more specimens from these and other horizons where, to date, none have been reported.

CLASSIFICATION OF THE CALYMENID TRILOBITES

The most extensive work on the taxonomy of the Calymenidae in recent times was done by Shirley (1936). His work was based primarily on the European, and especially the British, representatives of this family. This exhaustive study also included comparisons of the European species with those of North America, and the resulting taxonomic work was designed to include all genera of the Calymenidae. Therefore, it follows that any comprehensive study of this family which involves questions of taxonomy and morphology should be based on Shirley's work.

Shirley divided the Calymenidae into nine genera, five of which were new. Most of the splitting was done within the old genus *Calymene*, which was overcrowded with diverse forms and up to that time had acted as a catchall for anything which resembled those with the actual characteristics of *Calymene*, sensu stricto. The proposed genera were, in the order given: *Synhomalonotus* Pompeckj, 1898; *Flexicalymene* Shirley, 1936; *Reacalymene* Shirley, 1936; *Gravicalymene* Shirley, 1936; *Metacalymene* Kegel, 1927, emend.; *Platycalymene* Shirley, 1936; *Calymene*, sensu stricto, Brongniart, 1822; *Diacalymene* Kegel, 1927, emend., and *Papillicalymene* Shirley, 1936. Of these, all but two, according to Shirley, have Middle and/or Upper Ordovician representatives. These two are *Calymene* and *Papillicalymene*, which are Silurian and Devonian forms. As a result of this study, only *Calymene* can truly be said to have no known Ordovician representatives, since a new species from the Ogontz member of the Stonington beds has been referred questionably to *Papillicalymene* by the authors.

In his classification, Shirley based his generic divisions on the following features: number of thoracic segments when present, nature and shape of the glabella, nature and shape of the preglabellar field, including the presence or absence of a subsidiary ridge or rolled border on this structure, nature of the axial furrows, and the presence or absence of "papillate" glabellar lobes and corresponding buttresses on the fixed cheeks. This last character is considered most important in the classification. Based on the

presence or absence of the "papillate" lobes and buttresses, all of his genera are placed into one of two groups (except *Synhomalonotus*), those without these features (Group A), and those with them (Group B). Group B includes *Calymene*, *Diacalymene*, and *Papillicalymene*.

Many North American workers have accepted this classification, even though some of the genera are either not represented or have not been discovered in this region. The authors also accept this classification generally and find that the characters upon which Shirley bases his new genera are definitely of generic significance.

The writers object, however, to the use of the term "papillate," at least in the sense Shirley uses it. In this country, this term means "covered with papillae" or "having the shape of a papilla." Both meanings have accepted usage in paleontology. Shirley evidently had the latter in mind when he wrote the following:

> It will be noticed that the shape of the lobes in most upper Bala and Silurian species is papillate in correlation with the production of buttresses on the fixed cheeks. The second lobes and the extensions from the fixed cheeks bridge over the axial furrows and at this point are in contact.

However, it will be noted from Shirley's illustrations that these "papillate" lobes are not noticeably any different in general form from the mediolateral lobes of "non-papillate" species, and in the opinion of the authors, are not especially papilla-shaped. Apparently, he refers to the condition whereby the lateral lobes, usually the mediolateral, bridge the axial furrow and come in contact with prominant buttresses developed on the fixed cheeks. The authors suggest that the condition be stated as such, or a more descriptive term be coined for this condition, and that the term "papillate" be abandoned in this respect and left with only its original meanings.

The Middle and Upper Ordovician Calymenidae of Michigan, with one exception, are placed in the genus *Flexicalymene* and possess its characteristic features: 13 segments in the thorax, a subparabolic to bell-shaped glabella, and a prominent preglabellar field which is stretched forward or recurved, and which does not bear a subsidiary ridge. No prominent buttresses are developed on the fixed cheeks, and the lateral glabellar lobes are not in contact with the cheeks. Only in *Flexicalymene praelongicephala*, n. sp., from the lower Richmond rocks of Limestone Mountain in southeast Houghton County, Michigan, is there any deviation. In this species, the posterolateral glabellar lobes are so expanded that they push against the free cheeks, causing them to curve laterally, and coming in contact with them at the base of the axial furrows. The axial furrows at this point are very narrow and relatively shallow. There are no buttresses developed, however, and the lobes do not bridge the furrows but have grown against the fixed cheeks in the basal region of the axial furrows, and in doing so have made them noticeably shallower than normal for other members of the genus.

The one exception mentioned previously is a strange form from the Ogontz member of the Stonington beds exposed on the eastern side of Little Bay de Noc. This trilobite, the only calymenid form found in the Ogontz, has been placed in the genus *Papillicalymene* and given the name *P. husseyi*, n. sp. The specimen is referred to this genus because of the well developed buttresses on the fixed cheek opposite the frontal, anterolateral, and mediolateral glabellar lobes. The species also lacks a subsidiary ridge on the recurved preglabellar field, another character which it shares in common with typical species of *Papillicalymene*.

SYSTEMATIC DESCRIPTIONS

Phylum ARTHROPODA
Class TRILOBITA
Order PROPARIA

Family CALYMENIDAE Milne-Edwards, 1840
Genus FLEXICALYMENE Shirley, 1936
FLEXICALYMENE SENARIA (Conrad)
Pl. 123, figs. 1–11

Calymene senaria CONRAD 1841, p. 38, 49; Hall, 1847, p. 238, pl. 64, figs. 3a–n. *Flexicalymene senaria* (CONRAD) WHITTINGTON, 1941, p. 493.

Remarks.—Numerous descriptions of *Flexicalymene senaria* have been published and it would be superficial to offer another one here. The reader is referred to the excellent description of Whittington (1941, p. 493).

Flexicalymene senaria is common in Michigan in beds of Trenton age, and typical examples of this species from the Chandler Falls, Groos Quarry, and Collingwood members are illustrated for comparison with Hall's New York specimen, which they resemble closely. Notable differences in the degree of tuberculation appear to be a function of the conditions of preservation, and close examination reveals that most specimens are ornamented in the same general manner.

In Conrad's original description of *F. senaria*, no primary type was designated and no locality given. This species was first illustrated by Emmons (1842, p. 390) and later described in detail and illustrated by Hall (1847, p. 238). None of these workers established a primary type.

The authors have illustrated as representative of this species the complete, unrolled specimen first illustrated by Hall (1847, pl. 64, figs. 3a–c) from the Trenton group at Watertown, New York. The preservation of the specimen and the matrix in which it occurs suggest that it was collected from the Sherman Fall limestone.

Occurrence.—Middle Ordovician; Trenton group, New York, Appalachian region, Michigan, and other localities in east-central North America.

Hypotypes.—No. 84311, American Museum of Natural History, and Nos. 30065, 30068, 34225, 34226, and 34227, Museum of Paleontology, University of Michigan.

FLEXICALYMENE sp. cf. F. SENARIA (Conrad)
Pl. 124, fig. 13

Discussion.—A single cranidium found in the Groos Quarry limestone near the type section appears to be very typical of *F. senaria* except in one respect. The tuberculation on this specimen is very coarse, especially on the glabella and occipital ring. The individual tubercles are twice the size of those normally found on *F. senaria*, and are closer to those found on certain specimens of *F. croneisi*. Some normal variation in tuberculation is to be expected in any species, but not of this magnitude. The authors consider this specimen to be closely related to *F. senaria* on the basis of otherwise identical morphological characteristics.

Location.—Middle Ordovician; Trenton formation, Groos Quarry member, Groos Quarry, one mile north of Escanaba, Delta County, Michigan.

Hypotype.—A complete cranidium. No. 34246, Museum of Paleontology, University of Michigan.

FLEXICALYMENE SENARIA PARVICEPHALA, n. var.
Pl. 123, fig. 16

Description.—Cephalon semicircular, moderately convex, small, unusually wide, with width twice the length or greater. Glabella very short, wide, moderately convex but with flattened dorsal surface and with three pairs of lateral glabellar lobes, increasing in size posteriorly. Width across posterolateral glabellar lobes equalling length of entire glabella. Entire cephalon with large scattered tubercles, some bearing openings for sensory hairs.

Median lobe of glabella wide and flat, tapering slightly posteriorly, with coarse tuberculation. Frontal lobe broadly rounded, very short, rising steeply from preglabellar furrow. Anterolateral glabellar furrows distinct, narrow, shallow, anterolaterally directed. Anterolateral glabellar lobes small, convex, rounded, node-like, well developed, laterally directed, and separated from the flat medial lobe by very shallow saddles.

Mediolateral glabellar furrows moderately deep and wide, laterally directed, short. Mediolateral lobes very round, convex, laterally directed, separated from median lobe by relatively narrow, shallow saddles.

Posterolateral glabellar furrows deep, moderately wide, bifurcating medially, with principal branches directed posteriorly and medially inside the posterolateral lobes. Shorter branches directed anteriorly behind the mediolateral lobes. No intermediate lobes developed, but median lobe slightly expanded between the two branches on each side. Posterolateral lobes more rounded than in typical *F. senaria*, coarsely tuberculate, convex, separated from median lobe by shallow constricted saddles.

Axial furrows moderately deep, slightly convex laterally, shallower opposite anterolateral and mediolateral lobes. Antennary pits indistinct. Occipital furrow moderately deep and narrow behind median lobe, wider

and deeper behind posterolateral glabellar lobes, well defined on cheeks. Occipital ring yoke-shaped, but narrower behind median lobe than that of typical *F. senaria.*

Preglabellar field moderately wide, upturned at about 25°, bearing coarse tuberculation. Field not rolled or ridged. Preglabellar furrow moderately deep and wide.

Fixed cheeks slightly longer anteriorly than glabella, and relatively flat. Palpebral lobes low, extending from anterolateral glabellar lobes almost to the posterolateral furrow. Genal angles relatively sharp.

Thorax and pygidium unknown.

Remarks.—Although this specimen resembles typical *F. senaria* in most major respects, it possesses sufficient distinct characters to warrant varietal differentiation. This variety differs from *F. senaria* in the shortness of the cephalon and the glabella and in the relative ratio of the length to the width in these structures. It is further distinctive in the sparse, but coarse tuberculation, in having the glabella shorter than the fixed cheeks, and in the nature and size of the frontal lobe, which is shorter and more broadly rounded. The anterolateral glabellar furrows are much better developed than the corresponding structures in *F. senaria.* The preglabellar field does not jut markedly beyond the general anterior curvature of the cephalon and the entire cephalon, especially the fixed cheeks, is less convex.

Occurrence.—Middle Ordovician; Trenton formation, Groos Quarry just above the pelecypod horizon, at station 12 of Hussey (1936, p. 251), Delta County, Michigan.

Type.—Holotype, a nearly complete cephalon, No. 34228, Museum of Paleontology, University of Michigan.

FLEXICALYMENE QUADRICAPITA, n. sp.
Pl. 123, figs. 2–16

Description.—Cephalon semicircular, sharply truncated anteriorly, moderately convex. Dorsal surface tuberculate with exception of palpebral lobes. Tubercles of many sizes, with numerous small ones between more isolated large ones. Cephalon extremely wide for genus. Glabella only moderately convex, bell-shaped, more elongate and narrower than that of *F. meeki,* subquadrate anteriorly, and possessing three pairs of lateral glabellar lobes, increasing in size posteriorly.

Medial lobe of glabella elongate, narrow, widest anteriorly, tapering only slightly posteriorly, moderately convex, elevated only slightly above the level of the eyes and lateral lobes. Lobe becoming quite flat dorsally. Frontal lobe large, long, subquadrate, convex, rising sharply from preglabellar furrow. Anterior border truncated, wide, sides parallel. Angle between anterior and lateral borders sharply rounded. Surface strongly tuberculate.

Anterolateral glabellar furrows distinct, moderately deep, laterally directed, occurring more posteriorly than normal for genus. Anterolateral glabellar lobes very small, convex, rounded, well defined, directed laterally and very slightly anteriorly, strongly tuberculate, nearly continuous with medial lobe, separated only by a slight depression. Width across anterolateral lobes equal to or less than that across frontal lobe.

Mediolateral glabellar furrows deep, narrow, well defined, directed anterolaterally, not bifurcated. Mediolateral glabellar lobes strongly rounded, convex, tuberculate, smaller than normal, directed laterally and slightly anteriorly, separated from medial lobe by shallow but well defined saddles.

Posterolateral glabellar furrows deep and narrow, bifurcating, with strongest branches directed posteriorly along the inner edge of posterolateral glabellar lobes. Anterior branches short and shallow, directed behind mediolateral glabellar lobes. Slight suggestion of intermediate lobes between the branches. Posterolateral glabellar lobes very large, convex, longer than wide, rounded, but suggestive of a quadrilateral outline. Rounding greater than in *F. meeki* and others. Surface of lobes tuberculate, with largest tubercles on dorsoanterior and lateral margins.

Axial furrows of cephalon noticeably curved due to large size of posterolateral glabellar lobes and relatively small size of mediolateral lobes. Furrows deep, narrow, well defined. Antennary pits located well forward, almost at anterolateral edges of frontal lobe, at the intersection of the axial and preglabellar furrows. Occipital furrow deep and narrow behind posterolateral lobes due to posterior elongation and rounding of

these lobes, which fit snugly into concave depressions in the yoke-shaped occipital ring. Furrow becoming shallow behind medial lobe of glabella and on posterior margins of fixed cheeks, becoming very wide and nearly indistinguishable near lateral borders. Occipital ring more convex than normal for genus, especially behind medial lobe where ring is very wide.

Preglabellar field wide, very short, and sharply upturned, forming deep preglabellar furrow in front of both glabella and fixed cheeks. Furrow in front of fixed cheeks bending slightly anteriorly. Field tubuerculate, especially around frontal edge. No subsidiary ridge developed.

Free cheeks absent. Fixed cheeks broadly convex, rising sharply from the axial and preglabellar furrows but becoming quite flat and wide dorsally. Cheeks coarsely tuberculate, exceptionally wide at genal angles. Facial sutures diverging slightly behind anterior border, passing in back of eyes, then turning sharply toward anterolateral margin for a short distance before curving posteriorly to genal angles.

Eyes opposite mediolateral glabellar lobes. Lateral distance between palpebral lobes and axial furrows very large, twice that of *F. meeki*. Palpebral lobes elongate, moderately convex, not tuberculate, extending from a line bisecting anterolateral lobes posteriorly to a point slightly behind posterolateral furrows.

Thorax and pygidium not definitely known. Scattered thoracic segments in same strata identical with those of *F. meeki*, but slightly narrower. Isolated pygidia, with seven definite axial segments and suggestion of an eighth, found in some beds. Axial lobe narrow and very convex, nearly reaching posterior border. Axial furrows deep. Pleural lobes broadly convex, with five segments, and commonly with a shallow furrow extending from one-half to entire length of each segment. Lateral and posterior borders of some pygidia thickened, forming narrow but heavy brim. Segmentation of pygidium often obscured by marginal thickening, becoming obsolete near lateral borders.

Remarks.—Among the known species of *Flexicalymene*, *F. quadricapita* most nearly resembles *F. abbreviata* (Foerste). The two are similar in that they both possess a quadrate frontal lobe, a relatively flat glabella, large posterolateral lobes, a thick, convex occipital ring, and eyes located opposite the mediolateral lobes.

The two are strikingly different, however, in that *F. abbreviata* has a broadly rounded anterior margin. The margin of *F. quadricapita* is sharply truncated and may even be slightly concave anteriorly. The eyes of Foerste's species are located close to the axial furrows as in *F. meeki* (see pl. 123, figs. 18–20), and low, blunt projections are developed on the fixed cheeks opposite the anterior border of the frontal lobe. The eyes of *F. quadricapita* are widely separated, and the palpebral lobes relatively distant from the axial furrows in every specimen observed. There are no blunt buttresses developed opposite the lateral extensions of the frontal lobe. The deep preglabellar furrow extending in front of the fixed cheeks of *F. quadricapita* is directed laterally and anteriorly, while that in *F. abbreviata* is directed posteriorly and laterally. The lateral glabellar lobes form another basis for differentiation. In *F. quadricapita* the anterolateral lobes are smaller, rounder, and laterally directed. The posterolateral lobes are longer than wide, rounded, and fit snugly into depressions in the occipital ring. In *F. abbreviata* the frontal lobe is elongate, anteriorly directed, and better developed. The third lobe is round but not oblong, smaller, and does not press tightly against the occipital ring. Finally, the frontal lobe of *F. quadricapita* is larger and longer, but has sharply rounded corners. These corners in *F. abbreviata* are more angular.

F. quadricapita also resembles *F. meeki retrorsa* (Foerste) superficially, but in the latter species the eyes are opposite the anterolateral lobes and mediolateral furrows, and are very close to the axial furrows. The anterolateral lobes, in addition, are very well developed, elongate, and anteriorly directed, while the posterolateral lobes are subquadrate and laterally elongate, and the occipital furrow behind them is wide. Finally, the cephalon, and especially the glabella, of *F. meeki retrorsa* is very convex compared to that of *F. quadricapita*, which rises only slightly above the level of the cheeks and palpebral lobes. A cranidium of *F. meeki retrorsa* is illustrated for comparison (see pl. 123, fig. 1).

The only European form in any way com-

parable to *F. quadricapita* is *F. caractaci* (Salter), which is very similar in convexity of glabella, the expansion of frontal lobe, and the shape of the anterolateral and mediolateral glabellar lobes. Here the similarity ceases, however, since this form also has a rounded anterior border, a wider preglabellar field which is not as reflexed, an expanded but very rounded frontal lobe, smaller posterolateral lobes, and a much narrower occipital ring.

Occurrence.—Upper Ordovician; Lower Richmond(?), Bill's Creek shales at Ensign, and at Bill's Creek, Delta County; questionably at Limestone Mountain, Houghton County, layer VI of Case & Robinson (1915), Michigan.

Types.—Holotype, a well preserved cranidium No. 9916; paratypes, No. 30066, 34229, 34330, 34331, 34332, 34333, 34334, 34335, 34336, 34337, 34338, 34339, 34340, 34341, Museum of Paleontology, University of Michigan.

FLEXICALYMENE PRAELONGICEPHALA, n. sp.

Pl. 123, figs. 14–15

Description.—Entire cephalon unknown, apparently semicircular, moderately convex, with flat anterior border. Glabella moderately convex, very elongate, longer than fixed cheeks, broad anteriorly. Tuberculation unknown. Medial lobe of glabella subrectangular, straight sided, uniformly convex, rising abruptly from axial furrows and elevated well above rest of cephalon. Posterior width only slightly less than anterior. Frontal lobe quadrate, extremely large and long, bluntly rounded anteriorly, with parallel sides. Angles between anterior and lateral borders sharp. Width of frontal lobe greater than across anterolateral glabellar lobes.

Anterolateral furrows placed well back on glabella, elevated on side of medial lobe, not reaching base. Furrows very short, shallow, but distinct, laterally directed. Anterolateral glabellar lobes very small, indistinct, subrounded, moderately convex, but scarcely projecting laterally, located high on sides of medial lobe.

Mediolateral glabellar furrows short, moderately deep, wide, slightly curved and directed strongly anterolaterally. Mediolateral glabellar lobes suboval, convex, longer than wide. Lobes rising abruptly from axial furrows, separated from medial lobe of glabella by shallow, slightly constricted saddles.

Posterolateral glabellar furrows deep, narrow, bifurcating. Unbranched parts directed laterally and anteriorly. Principal branches long, deep, directed posteriorly inside posterolateral lobes and continuous with deep, constricted saddles separating these lobes from medial part of glabella. Secondary branches of furrows short, shallow, broad, directed anteriorly inside and behind mediolateral glabellar lobes. No intermediate lobes developed. Posterolateral glabellar lobes very large, subrounded to subhexagonal, moderately convex, anteriorly-posteriorly elongate.

Axial furrows deep, wide, strongly curved around posterolateral lobes. Slight suggestion of antennary pits opposite lateral extensions of frontal lobe produced by widening of axial furrows. Occipital furrow observed only behind glabella. Furrow deep and narrow behind posterolateral glabellar lobes, becoming shallower and still narrower behind medial lobe. Occipital ring yoke-shaped, thick, especially behind medial lobe.

Preglabellar field short, sharply elevated in front of glabella. Terminal margin of field sharply rounded, with no subsidiary ridge. Preglabellar furrow deep, narrow, well defined, very broadly curved, directed laterally and slightly anteriorly in front of fixed cheeks.

Fixed cheeks slightly to moderately convex, shorter than glabella. Free cheeks not observed. Facial sutures extending back from anterior border, diverging slightly and passing behind eye. Peripheral parts of sutures not observed. Eyes opposite mediolateral glabellar lobes. Palpebral lobes semicircular, slightly convex, rising slightly above level of cheeks, extending from a line biesecting the anterolateral lobes to a point slightly posterior to the posterolateral furrows.

Three pygidia found in association with cranidium apparently similar to that of *F. meeki*. Axial lobe very convex, with seven segments, extending nearly to posterior border. Pleural lobes moderately convex, with five ungrooved segments. Axial furrows deep. Slight thickening of posterior border just behind axial lobe, as in *F. quadri-*

capita, but not as well developed. Pygidium covered with closely set, small tubercles.

Remarks.—*F. praelongicephala* occurs in the same beds as *F. quadricapita* and resembles it more than any other species of *Flexicalymene*. The two are similar in general appearance. They both possess a somewhat quadrate frontal lobe and reduced, rounded anterolateral lobes. The eyes are in the same position in both, opposite the mediolateral lobes. The posterolateral lobes and the occipital ring are mutually expanded.

However, there is a marked difference in the size and elongation of the glabella, this structure being almost one third longer in *F. praelongicephala*. In addition, although both species have reduced anterolateral lobes, the reduction in *F. praelongicephala* is extreme. The lobes are located high on the medial portion of the glabella, not extending laterally beyond the parallel sides of the medial lobe. The mediolateral glabellar lobes are also reduced in *F. praelongicephala*, a condition not well developed in *F. quadricapita*, and the frontal lobe of the former, although also quadrate, is longer and more expanded.

There is some difference in the character of the preglabellar field, which is not as reflexed in *F. praelongicephala* as in *F. quadricapita*. Consequently, the preglabellar furrow in the latter species is deeper and narrower, and the anterior border sharply truncated or even slightly concave when viewed dorsally. The anterior margin of the former is broadly rounded.

Finally, the glabella of *F. praelongicephala* is very convex and elevated well above the level of the palpebral lobes and fixed cheeks. Although the sides of the glabella in *F. quadricapita* are equally as steep, the dorsal surface is very flat, extending only slightly above the level of the palpebral lobes.

Occurrence.—Upper Ordovician; Lower Richmond, layer VI of Case & Robinson (1915); Limestone Mountain, Houghton County, Michigan.

Types.—Holotype, an incomplete cranidium with the glabella, preglabellar structures, occipital ring and part of the right fixed cheek, No. 34242; paratype, a complete pygidium, No. 34243, Museum of Paleontology, University of Michigan.

FLEXICALYMENE PLANILABRA, n. sp.
Pl. 124, figs. 19–20

Description.—Cephalon semicircular, very convex, with granular surface. Glabella very short, convex, rising abruptly above flat preglabellar field and slightly overhanging it. Glabella slightly longer than fixed cheeks, anterior border strongly rounded. Medial lobe of glabella widest anteriorly, tapering slightly posteriorly, very convex. Three pairs of lateral glabellar lobes present; anterior pair smallest; posterior pair largest.

Frontal lobe not well defined, grading into laterally directed anterolateral glabellar lobes with hardly any trace of anterolateral furrows. Anterolateral glabellar lobes low, rounded, laterally elongate, not rising abruptly from axial furrows but sloping gently into them. Size of lobes comparable to those in *F. senaria*.

Mediolateral glabellar furrows directed slightly anteriorly and laterally, curved, deep and wide. Mediolateral glabellar lobes nodose, rounded laterally, separated from medial lobe of glabella by very pronounced constricted saddles.

Posterolateral furrows deep, well defined, broadly bifurcating, with strongest branches directed posteriorly around the front and inner margins of the posterolateral lobes. Anterior branches broad, short, directed behind mediolateral lobes. Posterolateral glabellar lobes large, very convex, subquadrate, with rounded anterior margins. Lobes connected to medial lobe of glabella by broad, shallow saddles.

Axial furrows well defined, deep and narrow posteriorly, becoming wider anteriorly. Antennary pits located opposite lateral extensions of frontal lobes and just anterior to anterolateral glabellar lobes. Pits very deep, extremely well defined. Occipital furrow very shallow behind medial lobe of glabella, becoming deep and narrower behind the posterolateral glabellar lobes.

Preglabellar field very long, constituting two-fifths of entire length of cranidium. Field extending straight outward, bending slightly upward near anterior margin of cranidium, with anterior part projecting strongly when viewed dorsally. No subsidiary ridge present. Preglabellar furrow broad, not deep.

Fixed cheeks triangular, very convex, with slight suggestion of buttresses opposite anterolateral glabellar lobes. Eyes opposite mediolateral glabellar lobes. Palpebral lobes low, extending from a line bisecting anterolateral lobes to the posterolateral furrows.

Thorax and pygidium unknown.

Remarks.—This species is quite unique in its morphological character, although it probably is related to the group centered around *F. senaria.* It resembles this species most in the glabella and the position of the eyes and palpebral lobes. However, the character of the preglabellar field, the size, the brevity of the glabella, and the extreme convexity of the entire cranidium, especially the medial lobe of the glabella, serve to distinguish it from the more common Middle Ordovician form.

F. gracilis (Slocom) is also morphologically similar in some respects. In this species the preglabellar field is flat and only slightly elevated, and the glabella is short. But the shape of the field is radically different. It is very wide, and the anterior border is broadly rounded, whereas in *F. planilabra* the field is much narrower, but relatively longer, and strongly rounded. In addition, the glabella of the Michigan form appears to be much more convex and the preglabellar furrow is not deep as it is in Slocom's species. The frontal lobe is more strongly rounded in *F. planilabra* and the antennary pits are exceptionally well developed.

One European form, *F. cambrensis* (Salter), possesses a flat preglabellar field with a shallow furrow, a short glabella, and deep antennary pits. However, this species also has a distinct furrow above the antennary pit, a suggestion of a fourth lateral lobe, and a broadly rounded frontal lobe. In the Michigan species, the first two structures are not present, and the frontal lobe is relatively longer and strongly rounded. In addition, the glabella is more convex and relatively shorter.

Occurrence.—Middle Ordovician; Trenton limestone; Sun Oil Company, Buss-Halb unit No. 1 well core, SWSENW sec. 8/T.3S/R.4E., Freedom Township, Washtenaw County, Michigan, from a depth of 3,975 feet.

Type.—Holotype, an incomplete cranidium with the glabella, preglabellar field, and right fixed cheek, No. 34244, Museum of Paleontology, University of Michigan.

FLEXICALYMENE CRONEISI (Roy)
Pl. 124, fig. 12

Calymene croneisi ROY, 1941, p. 160–161, fig. 124 a–d.

Flexicalymene croneisi (ROY) WHITTINGTON, 1954, p. 147–148, pl. 62, figs. 13–15.

Discussion.—Good descriptions and illustrations of this species are given by Roy (1941, p. 160–161, fig. 124a–d) and Whittington (1954, p. 147–149, pl. 62, figs. 13–15) and it is compared with *F. meeki, F. senaria,* and *F. fayettensis* by the latter author. Hence, only the relationship of the Michigan specimen to those found at Sillimans Fossil Mount in Baffin Land is discussed here.

Roy noted several similarities between *F. croneisi* and *F. senaria.* Whittington discussed additional similarities to *F. meeki* and *F. fayettensis.* These similarities are general, and are based on the outline of the glabella, the rounded preglabellar border, the general nature of the lateral glabellar lobes, and the nature of the axial and preglabellar furrows. *F. croneisi* shows additional affinities to *F. fayettensis* in possessing a low ridge on the preglabellar field, a glabella which is longer than it is wide, and in having the eyes in the same position.

Briefly, *F. croneisi* possesses the following distinctive characteristics: The length of the glabella is equal to that of the fixed cheeks anteriorly; a line joining the midpoints of the palpebral lobes passes through the posterior part of the anterolateral lobes; the glabella is narrower, and relatively longer than in *F. meeki, F. senaria,* etc., the maximum width being only 35 per cent of the maximum width of the cranidium, compared to 40 per cent for *F. meeki,* etc.; the maximum width of the glabella is less than the length; the preglabellar field possesses a low ridge; the frontal lobe slopes very abruptly into the preglabellar furrow, which is deep; the anterior border of the cephalon is sharply convex when viewed dorsally. In addition, the axial furrows of the cephalon are less divergent than in *F. meeki* and *F. senaria,* being almost parallel opposite the mediolateral and posterolateral lobes.

The Michigan specimen here identified as

F. croneisi resembles the holotype in almost every respect. The glabella of this specimen is slightly shorter than the fixed cheeks anteriorly, and the width of the glabella is 38.5% the total width of the cranidium, but otherwise the two are the same. One striking character which both Roy and Whittington failed to mention, and which the two specimens have in common, is the unusually coarse tuberculation on the cephalon. The authors note that the size of the tubercles in *F. croneisi* is twice that of those on *F. senaria*, *F. meeki*, and related forms, and consider this a distinctive characteristic.

The Michigan specimen is tentatively assigned to the Groos Quarry member of the Trenton formation. Since the original label has been inadvertently destroyed, this correlation is made on the lithology and faunal similarities of the containing matrix, and is believed correct. If this is true, the range of *F. croneisi*, originally described from rocks of Richmond age at Sillimans Fossil Mount, must be tentatively lowered to include the Middle Ordovician Groos Quarry formation.

Occurrence.—Middle Ordovician; Trenton formation, Groos Quarry member(?); Groos Quarry, 1 mile north of Escanaba, Delta County, Michigan.

Hypotype.—An incomplete cranidium, No. 34245, Museum of Paleontology, University of Michigan.

FLEXICALYMENE MAGNIPAPILLA, n. sp.
Pl. 124, fig. 17

Description.—Cephalon semicircular, only moderately convex, rounded anteriorly, with unusually coarse tuberculation. Glabella short, moderately convex, elevated above level of palpebral lobes and cheeks, bearing three pairs of lateral glabellar lobes of which the anterior pair are smallest and the posterior pair largest. Glabellar ornamentation distinct, with tubercles of several sizes covering entire surface. Largest tubercles high, conical, much larger than those in any other known species of *Flexicalymene*, some bearing openings for sensory hairs. Many distinct smaller tubercles present.

Medial lobe of glabella moderately convex, elevated above lateral lobes and eyes, rounded anteriorly, decreasing slightly in width posteriorly. Frontal lobe well rounded, rising gently from preglabellar furrow. Lateral extensions of frontal lobe triangular, width across them slightly less than width across anterolateral glabellar lobes.

Anterolateral glabellar furrows shallow, narrow, distinct, laterally directed. Anterolateral glabellar lobes exceptionally long, depressed at lateral extremities, strongly tuberculate, laterally directed, continuous with medial lobe of glabella.

Mediolateral glabellar furrows well defined, deeper than axial furrows, directed laterally and somewhat anteriorly. Mediolateral glabellar lobes subrounded, moderately convex, strongly tuberculate, depressed laterally, sloping gently into shallow axial furrows, separated from medial lobe of glabella by shallow but well defined saddle.

Posterolateral glabellar furrows deep, moderately wide, well defined and bifurcating at medial lobe. Principal branches deep, directed posteriorly along inner edges of posterolateral lobes. Anterior branches short, shallow, directed behind the mediolateral lobes. No intermediate lobes developed. Posterolateral glabellar lobes large, subquadrate, moderately convex, very coarsely tuberculate, separated from medial lobe by shallow constricted saddles.

Axial furrows well defined, deep at the antennary pits and around the frontal lobe, becoming very shallow opposite the anterolateral and mediolateral glabellar lobes, and deep again from the posterolateral glabellar furrows to their termination at the occipital furrow. Bottoms of furrows not tuberculate, sides finely papillate.

Antennary pits deep and well developed, located in the axial furrows opposite the lateral extentions of the frontal lobe. Occipital furrow finely tuberculate, shallow and wide behind the medial lobe of the glabella and on the fixed cheeks, deep and narrower behind the posterolateral glabellar lobes. Occipital ring unusual in its coarse tuberculation; largest tubercles very high and conical, suggesting low blunt spines. Ring yoke-shaped.

Preglabellar field rounded, reflexed at about 30°, finely papillate, projecting slightly beyond anterior margin of cephalon when viewed dorsally. Preglabellar furrow wide, moderately deep. Free cheeks incompletely preserved. Fixed cheeks noticeably longer than glabella, broadly convex, very

finely papillate except on anterior margins where scattered medium sized tubercles occur. Facial sutures poorly defined, passing almost straight back from anterior margin, behind eyes, turning laterally and posteriorly for a short distance, then sharply backward to the genal angles.

Eyes opposite anterolateral glabellar lobes. Palpebral lobes moderately convex, placed well forward on fixed cheeks, extending from a line passing just in front of anterolateral glabellar furrows to mediolateral furrows.

Thorax and pygidium unknown.

Remarks.—*F. magnipapilla* resembles *F. senaria* in general appearance, but differs from this species in many respects. The position of the eyes resembles that of *F. meeki* in being opposite the anterolateral glabellar lobes, and is very atypical of Middle Ordovician species. In addition, the glabella is shorter than the fixed cheeks, a condition not characteristic of *F. senaria*. The relationship between the lateral glabellar lobes and the axial furrows is unusual in *F. magnipapilla* and quite unlike any other form studied. The anterolateral and mediolateral glabellar lobes are depressed laterally and slope gradually into the axial furrows, which are correspondingly very shallow at these intersections. The anterolateral lobes are more elongate, and the anterolateral furrows distinct and better developed than in Conrad's species.

In addition, the very coarse tuberculation distinguishes *F. magnipapilla* from any other species of *Flexicalymene*. The largest nodes, or tubercles, especially those on the posterolateral glabellar lobes and occipital ring, are quite high and conical, resembling low spines (pl. 124, fig. 17).

Occurrence.—Middle Ordovician; Trenton formation, Chandler Falls limestone; Chandler Falls on the Escanaba River, Delta County, Michigan.

Types.—Holotype, a cephalon without the free cheeks, No. 34247, Museum of Paleontology, University of Michigan.

FLEXICALYMENE sp. cf. F. MEEKI (Foerste)
Pl. 123, fig. 17

Discussion.—A single pygidium from the Bill's Creek shale is very similar to that found in typical *F. meeki*. The pleural segments are wide, and most important, undivided. The axial lobe is moderately convex, with seven segments but no suggestion of an eighth as appears in some pygidia of *F. quadricapita*, with which this pygidium is associated. There is no thickening of the posterior rim, and the segmentation is clearly visible to the edge of the lateral borders. The laterally thickened rim found in some pygidia of *F. quadricapita* is not present.

As previously noted, no other fragments of *F. meeki* have been found in the Richmond beds of Michigan, and this form seems to have been replaced by *F. quadricapita*, n. sp., in both numbers and distribution. The authors can make no definite identification of this pygidium, and it may belong to an entirely different species. For the present, therefore, it will suffice to note its similarities to the pygidium of *F. meeki*, and to state that it resembles this species more than any other studied.

Occurrence.—Richmond group?, Bill's Creek shale, in railroad cut near Ensign, Michigan.

Figured specimen.—A complete pygidium, No. 34269, Museum of Paleontology, University of Michigan.

Genus PAPILLICALYMENE Shirley (1936)
PAPILLICALYMENE HUSSEYI, n. sp.
Pl. 123, fig. 18

Description.—Cephalon small, incomplete, but apparently semicircular in outline, with sharply truncated anterior border. Glabella short and wide, slightly longer than fixed cheeks anteriorly, moderately convex, rising abruptly from preglabellar and axial furrows, becoming flattened dorsally. Anterior border wide, nearly straight.

Medial glabellar lobe broad and flat, bearing low, rounded medial ridge and rising only slightly above level of the lateral lobes and fixed cheeks. Lobe widest anteriorly, gradually tapering posteriorly, wide for genus. Three pairs of lateral glabellar lobes present, occurring in a graded series with the anterior pair smallest and the posterior pair largest.

Frontal lobe short, rectangular, laterally very elongate. Lateral extensions terminating abruptly opposite well defined buttresses on fixed cheeks, but not joining them. Lat-

eral margins very flat, anterior margin broadly rounded, almost flat.

Anterolateral glabellar furrows well defined, moderately deep, unusually broad, laterally directed. Furrows appearing as deep notches in side of glabella when viewed dorsally. Anterolateral glabellar lobes broad and well defined medially, tapering to blunt rounded points laterally. Lobes convex, not definitely separated from medial lobe by furrows or saddles. Width across anterolateral lobes equal to, or less than that across frontal lobe.

Mediolateral glabellar furrows deep, wide, and directed anterolaterally. Mediolateral glabellar lobes convex, oval, elongate, directed anterolaterally, separated from medial lobe by broad, shallow, constricted saddles.

Posterolateral glabellar furrows deep, wide where they bifurcate medially but becoming narrow laterally in front of posterolateral lobes. Principal branches long, deep, directed posteriorly and medially inside posterolateral lobes. Anterior branches short, wide, directed behind mediolateral lobes. Distinct, broadly rounded intermediate lobes developed between branches of furrows. Posterolateral glabellar lobes subquadrate, convex, directed anterolaterally, with anterior angles acute and sharp. Width of lobes greater than length.

Axial furrows deep, broad, with steep sides, constricted by development of buttresses on fixed cheeks opposite frontal, anterolateral, and mediolateral glabellar lobes. Furrows diverging posteriorly, not curved. Antennary pits relatively shallow and broad, located beneath and slightly posterior to lateral projections of the frontal lobe.

Occipital furrow strongly curved, bending anteriorly behind medial lobe of glabella, where it is shallow and broad, diverging posteriorly and laterally behind posterolateral glabellar lobes, becoming deeper. Furrow wide on posterior part of fixed cheeks, becoming indistinct at lateral extremities. Occipital ring convex, yoke-shaped, relatively narrow behind posterolateral lobes, thickening considerably and more convex anteriorly behind medial lobe.

Preglabellar field wide, reflexed at about 45° well in front of glabella, leaving an unusually wide, deep, U-shaped preglabellar furrow which deepens at its intersection with axial furrows. Opposite this intersection, low nodes developed on upturned preglabellar field.

Free cheeks unknown. Fixed cheeks triangular, moderately convex, bearing well developed buttresses opposite lateral extensions of frontal lobe and low rounded buttresses opposite anterolateral and mediolateral glabellar lobes. Facial sutures indistinct, diverging slightly from anterior border, passing behind eyes to a point opposite anterior part of posterolateral lobes, then diverging laterally and anteriorly for a short distance before bending posteriorly to the genal angles.

Palpebral lobes poorly preserved, extending from a point opposite anterolateral lobes to a point slightly posterior to posterolateral glabellar furrows.

Thorax and pygidium unknown.

Remarks.—This specimen is referred to the genus *Papillicalymene* because of the well developed buttresses on the fixed cheeks opposite the frontal, anterolateral, and mediolateral glabellar lobes. The specimen also lacks a subsidiary ridge on the recurved preglabellar field, another character which it shares in common with typical species of *Papillicalymene.*

This classification is questionable however in that the specimen, an internal mold, is not actually "papillate" in the sense of Shirley. That is, the lateral extensions of the frontal lobe, the anterolateral and mediolateral glabellar lobes do not actually come in contact with the buttresses developed on the fixed cheeks opposite them, and hence do not bridge the axial furrow. Further, the lateral extensions of the frontal lobe and the corresponding anterior buttresses most nearly approach this situation, while the buttresses opposite the anterolateral and mediolateral lobes are only moderately developed and are relatively distant from the lobes. This situation is reversed in *Papillicalymene papillata*, the genotype species, where the anterolateral and mediolateral glabellar lobes intercept strongly developed buttresses, but the buttresses opposite the lateral extensions of the frontal lobe are small, and they do not join.

Two things must be considered, however.

First, the specimen is an internal mold. In the original state, with the exoskeleton intact, the lateral extensions of the frontal lobe, at least, probably came in contact with the most anterior buttresses, since they are only slightly separated in the mold. If they did, they probably bridged the axial furrow. There is some doubt as to whether the anterolateral and mediolateral lobes also accomplished this. Most likely it would depend on the thickness of the exoskeleton. Thus, the condition which Shirley calls "papillate" is reached, at least to some extent.

Secondly, buttresses are well developed opposite the frontal, anterolateral, and mediolateral lobes, not merely suggested. This condition is found only in *Papillicalymene* among the calymenid genera. In the others included in Group B of Shirley, only the mediolateral lobes have well developed buttresses opposing them.

The age of the Ogontz specimen must also be considered. Shirley denoted *Papillicalymene* as a Silurian genus, with no Ordovician representatives. If *P. husseyi* is correctly identified generically, it represents the oldest known member of this genus, and lowers the range of *Papillicalymene* considerably. This also suggests that the Michigan form is representative of the ancestral stock(s) which gave rise to the highly developed Silurian forms of the genus, and it should be noted that, compared to these forms, *P. husseyi* displays primitive characters.

The development of buttresses on the fixed cheeks and their subsequent interception of the lateral glabellar lobes is considered a morphological advance in the Calymenidae. This is well illustrated by the stratigraphic distribution of these forms, Upper Ordovician (as of this paper) to Silurian, with the majority of the forms occurring in the Silurian.

Even if the "papillate" condition was not reached in *P. husseyi*, this form was certainly approaching that condition, and in the frontal, anterolateral and mediolateral lobes, which strongly suggests its affinities to this genus. The fact that the frontal lobe reached this condition first in the Michigan form is hard to explain, since the lateral extensions of this lobe do not join the anterior buttresses in the Silurian forms. More than two species, however, are necessary for study before the lineage can be worked out. For the time being, this specimen must be placed in *Papillicalymene*, even though certain characters are lacking. The only other alternative would be to erect a new genus, and the authors do not approve of this action in light of the apparent affinities of this specimen with *Papillicalymene*.

The development of buttresses opposite the frontal, anterolateral, and mediolateral glabellar lobes, the probable attainment of a "papillate" condition (that is, a joining of the lateral lobes and the buttress, thus bridging the axial furrow) in the lateral extensions of the frontal lobe at least, and the lack of a subsidiary ridge on the uncurved preglabellar field are the principal basis for this assignment.

Hussey has suggested that the Stonington beds are boreal in origin, and that their fauna is distinct in many ways. The genus *Papillicalymene*, formerly known only from Europe, most likely would have reached the northern part of Michigan by means of a boreal invasion, possibly through Hudson Bay and thus supports this theory. It is the only calymenid trilobite known from these beds and is known only from the holotype.

Occurrence.—Upper Ordovician; Richmond group, Stonington beds, Ogontz member; East side of Little Bay de Noc, Michigan.

Type.—Holotype, a cranidium without the left fixed cheek, No. 9905, Museum of Paleontology, University of Michigan.

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HOLOTHURIAN SCLERITES FROM THE KENDRICK SHALE OF EASTERN KENTUCKY

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ABSTRACT—Sixteen species of holothurian sclerites are identified from the type locality of the Kendrick shale of the upper Pottsville in eastern Kentucky. Among the perforate plates, wheels, hooks, and buttons are one proposed new genus, *Petropegia*, and seven new species: *Thuroholia wanlessi*, *T. floydensis*, *T. irregularia*, *Petropegia radiata*, *P. spinosa*, *Etheridgella biconvexa*, and *Theelia hexacneme*. Two sclerite assemblages, which are believed to be original associations, were also recovered; one contains plates of several species, and the other, a wheel and a hook fragment, in addition to perforate plates.

INTRODUCTION

FROM material collected for a study of the various faunal elements of the early Pennsylvanian Kendrick shale of eastern Kentucky, a number of holothurians were recovered. They include some previously described forms, one new genus and seven new species.

In 1932 Croneis & McCormick published a review of the literature on fossil holothurian sclerites and advocated a form classification for these separated skeletal parts. More recently the group was extensively restudied by Frizzell & Exline (1955), who refined some of the earlier generic and specific definitions and introduced a number of new genera and species, the whole being grouped into a unified form classification similar to that used for the conodonts. This classification is used here, and with it the taxonomic procedures of Frizzell & Exline and others. The uncertain taxonomic position of these parts of organisms may be clarified in the near future as a result of a proposal by Moore & Sylvester-Bradley (1957) at the present time before the International Commission on Zoological Nomenclature.

STRATIGRAPHY

The Kendrick shale lies in the interval between the Amburgy (Williamson) and Whitesburg coals of the upper Breathitt (upper Pottsville) formation. It is one of the few fossiliferous marine units persistent enough in their characteristics to hold promise as aids in the correlation of Pennsylvanian beds in eastern Kentucky. It was orginally described by W. R. Jillson (1919) from a locality on Cow Creek, a tributary of the Levisa Fork of the Big Sandy River, in Floyd County, Kentucky.

Although the current study includes collections from a number of Kendrick outcrops in southeastern Kentucky, the holothurian sclerites recovered are all from the Cow Creek drainage area. A section beginning in the road cut opposite the "Ike" Gobel home, about one hundred yards downstream from the type locality, is given below:

7.	Sandstone, light gray to buff, micaceous, medium-grained; massive, irregularly cross-bedded.	8′–15′
	Unconformity	
	Kendrick shale	
6.	Shale, dark gray, calcareous, containing numerous ironstone concretions; sparsely fossiliferous.	3′
5.	Shale, dark blue-gray, calcareous, with abundant fossils; small calcareous concretions, many containing fossils; detrital plant remains common on bedding planes; weathers black.	15′
4.	Shale, brown, leached, and spongy in appearance; a few fossils, occurring chiefly as molds.	5′
3.	Shale, sandy, micaceous, grading upward into Unit 4.	0′6″–1′
2.	Covered interval (small gully on hillside showed coal streak—Amburgy?)	5′
1.	Sandstone, light gray to buff, micaceous, medium grained (exposed in bed of Cow Creek).	

FAUNA

Previous work.—Jillson's (1919) original description of the Kendrick marine shale contains a faunal list (p. 101–102) by Charles Schuchert. In 1931 W. C. Morse

presented a discussion of the Pennsylvanian faunas of Kentucky, including a revised faunal list for the Kendrick (p. 299–300) and descriptions of several new species from this horizon. Since then, Dunbar & Condra (1932) and Miller, Dunbar & Condra (1933) have described a number of new species from the brachiopods and nautiloid cephalopods of the Kendrick shale.

Faunal associations.—The megafauna of the Kendrick shale is dominantly a brachiopod-molluscan fauna; the prominence of the brachiopods is due for the most part to the presence of a large number of individuals of the genera *Marginifera* and *Chonetes*, whereas pelecypods and gastropods are represented by a number of genera as well as of individuals.

Cephalopods do not make up a large part of the thanatocoenose, but among them are a number of goniatites, which are generally rare in the Appalachian area. The preservation of the aragonite shell material of many of the mollusks is worthy of special note, and on some, particularly the cephalopods, the nacreous layer and color patterns also are preserved.

In addition to the brachiopods and mollusks, there are some solitary corals (apparently all *Lophophyllidium*), crinoid fragments and rare trilobite pygidia.

Among the microscopic forms are the holothurian sclerites; foraminifera (largely *Endothyranella*); bryozoan fragments; minute and immature pelecypods, gastropods and brachiopods; questionable ophiuroid skeletal parts; echinoid plates and spines; ostracods; a few scolecodonts and conodonts; and some spores.

Holothurian sclerites.—The holothurian remains—which include sieve plates, wheels, hooks and buttons—occur scattered on the bedding plane surfaces and are apparently concentrated in Unit 5 of the above section. They are generally disassociated, but in two instances a number of sclerites were found grouped together.

One of these assemblages (pl. 125, fig. 14) contains three types of sclerites: perforate plates, some of which are identifiable as *Thuroholia gutschicki* (Frizzell & Exline) and *T. mccormacki* (Frizzell & Exline); a wheel, *Protocaudina kansasensis* (Hanna); and the eye loop of a hook, *Achistrum* sp. Although it is barely possible that the association of these sclerites represents sorting on the sea floor, it seems reasonable to assume that all of these types are skeletal parts of one animal.

The assemblage may be of further value as it relates to the origin of the sclerites themselves, although this is a complex problem. Frizzell & Exline (1955, p. 84) point out that plates similar to *Eocaudina*, *i.e.*,

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EXPLANATION OF PLATE 125

Figures approximately ×40 unless otherwise noted

FIGS. *1,2—Achistrum ludwigi* (Croneis). *1*, nearly complete specimen (small fragment of spear missing). *2*, eye penetrated by shank of second hook.

3–7—Achistrum monochordata Hodson, Harris, & Lewison. Specimens showing variations in eye shape and in position of crossbar.

8—Achistrum brownwoodensis (Croneis).

9—Achistrum nicholsoni? Etheridge.

10–12—Etheridgella biconvexa, n. sp. *10*, thick, rounded specimen. *11*, flattened specimen with flange. *12*, holotype; U.K., Dept. Geology Coll., No. TC 97.

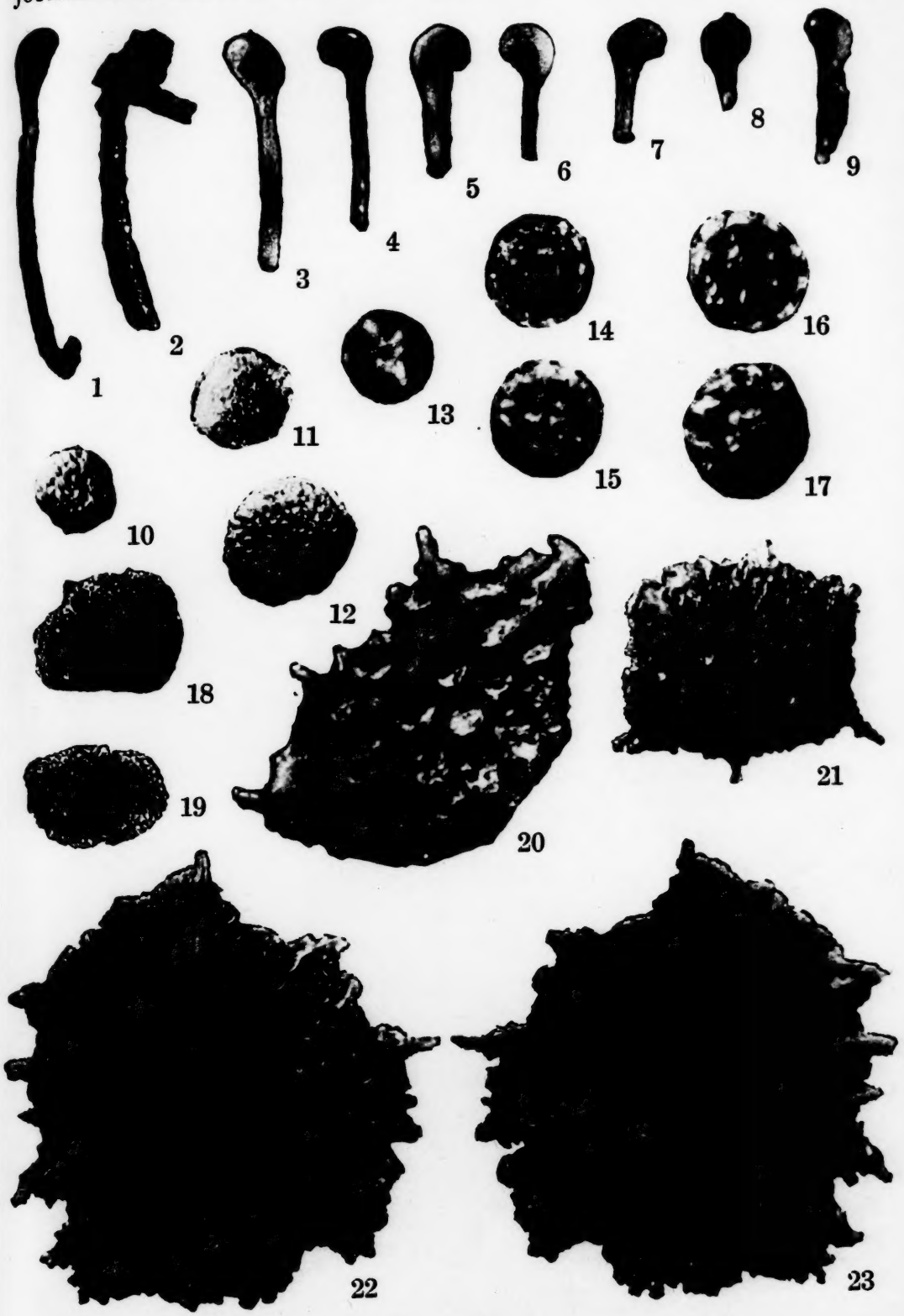
13—Theelia hexacneme, n. sp. Holotype, lower side, showing small nodes near center; U.K., Dept. Geology Coll., No. TC 111. ×100. (Retouched.)

14–17—Protocaudina kansasensis (Hanna). *14,16*, top views of specimens. *15,17*, bottom views of same specimens. ×66.

18,19—Thuroholia? sp. undt. Small plates with fine pitting.

20,21—Petropegia spinosa, n. sp. *20*, border of broken plate, showing spinose characteristic. *21*, holotype; U.K., Dept. Geology Coll., No. TC 95.

22,23—Petropegia radiata, n. sp. *22*, holotype, top view. *23*, holotype, bottom view. U.K., Dept. Geology Coll., No. TC 94. ×24.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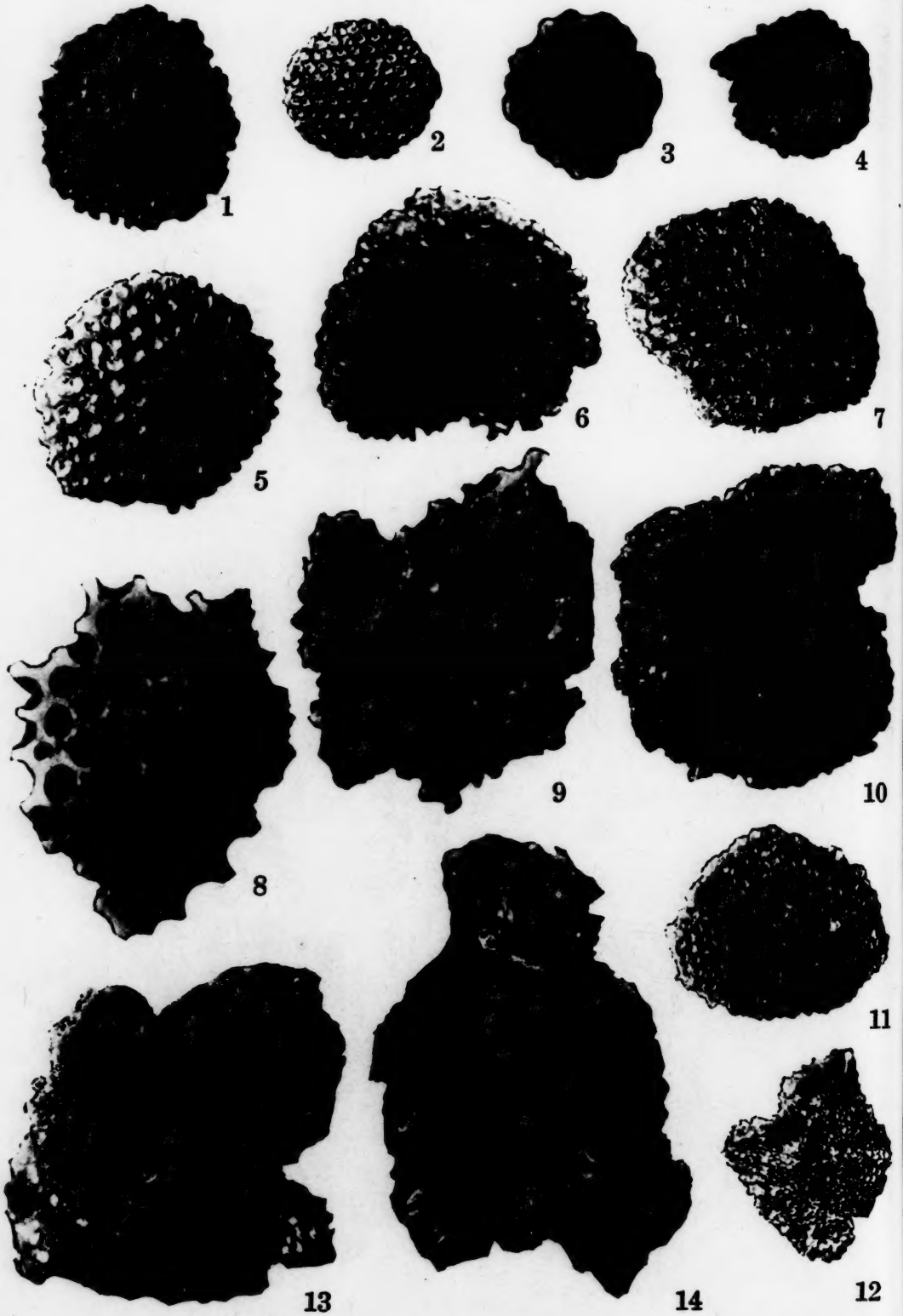
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Thuroholia (see below) are known from embryonic crinoids, and that, therefore, plates of this type cannot be regarded as unquestionably holothurian; yet the argument for the holothurian derivation of *Achistrum*, a form unknown in modern holothurians, seems to be based, in large part, on an occurrence (Etheridge, 1881, p. 187) in which a hook is cemented to perforate plates. Some have interpreted Etheridge's find as merely fortuitous. The assemblage from the Kendrick shale is evidence against this latter conclusion, but whether or not a natural association of wheels, hooks and perforate plates, proves, *per se*, a holothurian source for all these types, may still be debatable. In regard to the possibility that they are all skeletal parts of embryonic crinoids, it may be noted that no crinoids other than *Paragassizocrinus?* sp. have been recovered from the Kendrick.

The most successful method of recovering the sclerites was to pick them off the bedding surfaces with a needle. Methods which require disaggregation of the shale, washing and sieving were generally too severe to permit the fragile sclerites to come through unbroken.

SYSTEMATIC DESCRIPTIONS

Complete synonymies are given by Frizzell & Exline (1955) and are not repeated here. Listed are only those references which change or otherwise influence the taxonomy.

Phylum ECHINODERMATA
Class HOLOTHUROIDEA
Family CALCLAMNIDAE Frizzell & Exline, 1955
Genus THUROHOLIA Gutschick, 1954

Thuroholia GUTSCHICK, 1954, p. 827–829.
Eocaudina MARTIN, emend. FRIZZELL & EXLINE, 1955, p. 82–83.
Thuroholia LANGENHEIM & EPIS, 1957, p. 167.

Diagnosis.—Sclerites in the form of perforate plates, with cross sections flat, concavo-convex or plano-convex; single layered. Outline commonly circular, subcircular or hexagonal; less commonly elongate, subelliptical or irregular. Periphery smooth, scalloped or spinose. Perforations circular, elliptical or polygonal, varying in diameter, number and arrangement; most common arrangement in straight rows often aligned at about 120° to one another; less common, in somewhat concentric circles or without pattern. Surface smooth, uneven and sometimes slightly nodose. Diameter varies from 0.20 to 1.5 mm. or, since some of the larger forms suggest a broken border, probably more.

Type species.—*Thuroholia croneisi* Gutschick.

Remarks.—Frizzell & Exline (1955) regrouped holothurian sclerites according to their morphology, dividing the perforate plates into several genera. They emended one of these genera, *Eocaudina*, and designated *Eocaudina septaforaminalis* Martin as

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EXPLANATION OF PLATE 126

Figures approximately ×40 unless otherwise noted

FIGS. *1,5—Thuroholia wanlessi*, n. sp. *1*, Holotype, showing nodes in central area; U.K., Dept. Geology Coll., No. TC 86. *5*, slightly larger specimen, with raised central area.

2—Thuroholia mccormacki (Frizzell & Exline). Specimen with typical number, shape and pattern of perforations.

3,4—Thuroholia gutschicki (Frizzell & Exline). Specimens showing variation in size of perforations; fig. *3* is the more "open" type.

6,7—Thuroholia floydensis, n. sp. *6*, holotype; U.K., Dept. Geology Coll., No. TC 88. *7*, specimen showing a variant size of perforations.

8,9—Thuroholia croneisi Gutschick. Specimens showing typical large size of both plate and perforations.

10–12—Thuroholia irregularis, n. sp. *10*, holotype; U.K., Dept. Geology Coll., No. TC 90. *11*, specimen varying from holotype in regularity of size and arrangement of perforations. *12*, smaller specimen with greater curvature of plate.

13,14—Assemblages of holothurian plates. *13*, assemblage containing only perforate plates, *T. gutschicki* (Frizzell & Exline) and *T. mccormacki* (Frizzell & Exline). *14*, assemblage including three forms of sclerites: perforate plates—*T. gutschicki* and others; a hooked sclerite—*Achistrum* sp.; and a wheel—*Protocaudina kansasensis* (Hanna) (last two are just to right of center of figure); ×23.

the type species. Langenheim & Epis (1957, p. 167) point out that this choice was unfortunate, for the unbroken holotype *E. septaforaminalis* Martin was described as a wheel type sclerite rather than a perforate plate, and thus according to Frizzell & Exline's classification would belong in another family. Therefore, we are retaining the name *Thuroholia* Gutschick for the perforate plates rather than using *Eocaudina*.

Frizzell & Exline's treatment of the morphology of the genus *Eocaudina* places emphasis upon plate outline and pattern of perforations. In the current study, the outline of many specimens, especially of the larger plates, is uncertain because of breakage or apparent incomplete growth. A very useful characteristic for identification of some of these forms seems to be the size of the perforations and the uniformity or variation of their size.

THUROHOLIA CRONEISI Gutschick
Pl. 125, figs. 8,9

Thuroholia croneisi GUTSCHICK (in part) 1954, p. 829, text-figs. 5–7, 9–19.

Description.—Sclerites flat to slightly curved perforate plates, circular to elliptical in outline. Border smooth to deeply scalloped. Perforations generally circular to elliptical, varying in diameter and number: diameter ranges from 0.04 to 0.12 mm., number from 30 to 100; they tend to be aligned in rows about 120° apart.

Dimensions.—Greatest diameter, fig. 9, 1.42 mm.; fig. 8, 1.32 mm. Reported diameter for the species is 0.65 to 1.35 mm.

Remarks.—The figured specimens show broken edges, suggesting a diameter greater than the limit given in the species description. Figs. 8 and 9 illustrate some of the variation in the size of perforations in specimens assigned to this species.

T. croneisi Gutschick differs from *T. gutschicki* (Frizzell & Exline) in the greater number of perforations, their larger size, and their greater variation in size. The perforations of *T. croneisi* are larger and more varied than is characteristic of *T. mccormacki* (Frizzell & Exline). The perforations of *T. croneisi* are most similar to those of *Petropegia spinosa*, n. sp., except that *T. croneisi* has no bordering spines.

THUROHOLIA GUTSCHICKI (Frizzell & Exline)
Pl. 125, figs. 3,4

Eocaudina gutschicki FRIZZELL & EXLINE, 1955, p. 87, pl. 3, figs. 7–8.

Description.—Thin, flat perforate plates with a slightly scalloped, subcircular to somewhat hexagonal outline. Perforations about 0.04 mm. in diameter and smaller, arranged in straight rows with up to 6 to 8 in a row and typically 6 to 8 rather straight, parallel rows to a plate; diameter of perforations fairly constant within a plate but varying somewhat among specimens.

Dimensions.—Diameter of fig. 3, 0.62 mm.; fig. 4, 0.58 mm. Reported range of diameter from 0.4 to 0.7 mm.

Remarks.—*T. gutschicki* is the most common form of sclerite in this collection. Specimens assigned to the species are particularly consistent in general shape and are more uniform than most in diameter of perforations; however, two types may be distinguished—some having relatively thick walls between perforations, others thin. To some extent differentiation on basis of wall development also may be found in *T. mccormacki*.

In pl. 125, fig. 14, an assemblage of plates is illustrated. At least 8 of these are identifiable as *T. gutschicki*, but also included are several *T. mccormacki*, one *Protocaudina kansasensis* and a fragment of *Achistrum* sp. The possible significance of this assemblage as it bears upon the holothurian origin of these plates is discussed above.

THUROHOLIA MCCORMACKI (Frizzell & Exline)
Pl. 125, fig. 2

Eocaudina mccormacki FRIZZELL & EXLINE, 1955, p. 87–88, pl. 3, fig. 9.

Description.—Sclerites in form of perforate plates; sub-circular to somewhat hexagonal in outline; flat, thin. Perforations fine, of nearly equal size, about 0.01 mm. in diameter; in straight rows with about 10 perforations to a row and typically 10 to 12 rows to a plate.

Dimensions.—Greatest diameter of figured specimen, 0.68 mm. Reported range in diameter, 0.56 to 0.62 mm.

Remarks.—*T. mccormacki* is one of the

more common forms in this faunule. Many of the specimens are complete, and among the individuals there is little variation in pattern or size of perforations. This sclerite is distinguished from *T. gutschicki* by the smaller diameter of the perforations, the greater number of perforations per row, and the greater number of rows per plate.

THUROHOLIA WANLESSI, n. sp.
Pl. 125, figs. 1,5

Description.—Sclerites in form of perforate plates, nearly circular, thicker than most, plano-convex with the central part 2 to 3 times the thickness of the outer edge; periphery uneven or slightly scalloped. Perforations subcircular to somewhat hexagonal, of consistent size, 0.04 mm. in diameter; in straight rows at 120° angle, with 10 or 11 perforations in a row and 12 or 13 rows to a plate.

Dimension.—Greatest diameter of holotype (fig. 1), 0.89 mm.

Types.—Deposited in University of Kentucky, Department of Geology Collection. Holotype No. TC 86.

Remarks.—In some specimens the upper surface of the central area has small nodes, but these do not seem persistent enough to be considered a specific characteristic. The absence of nodes may be due to immaturity, for they are missing on the smaller forms. Resembling *T. mccormacki* in perforation arrangement, *T. wanlessi* differs in being larger, in having larger perforations, and particularly in having a plano-convex cross section. Although the species is represented in this collection by several specimens, it is less common than *T. gutschicki* or *T. mccormacki.*

THUROHOLIA FLOYDENSIS, n. sp.
Pl. 125, figs. 6,7

Description.—Perforate plates with roughly subcircular outline, typically flat but occasionally gently curved, edges moderately straight to broadly scalloped. Perforations subcircular to polygonal, medium to small size, ranging in diameter from 0.03 mm. to 0.05 mm.; larger perforations in central portion of plate where arranged in generally straight rows about 120° apart; toward margin perforations become smaller, less well developed and irregular. Number of perforations varies from approximately 100 to 130 to a plate.

Dimension.—Greatest diameter of holotype (fig. 7), 1.4 mm.

Types.—Deposited in University of Kentucky, Department of Geology Collection. Holotype No. TC 88.

Remarks.—This species varies somewhat from specimen to specimen in details of plate outline and perforation pattern, but within the limits as described it is recognizably consistent. It is easily distinguished from *T. croneisi* by the size and shape of perforations, from *T. gutschicki* and *T. mccormacki* by the size and number of perforations and the lack of regularity in their arrangement.

THUROHOLIA IRREGULARIS, n.sp.
Pl. 125, figs. 10–12

Description.—Sclerites in form of perforate plates; surface somewhat undulating or nodose; outline irregular and variable. Perforations numerous and irregularly distributed, fine but varying in size, smaller in central portion of plate and larger toward margins; maximum diameter 0.03 mm.

Dimensions.—Greatest diameter of holotype (fig. 10), 1.57 mm. Range of specimens studied, 0.8 to 1.57 mm.

Types.—Deposited in University of Kentucky, Department of Geology Collection. Holotype No. TC 90.

Remarks.—Species characterized by its large size and numerous fine perforations. The outline of all specimens studied is somewhat irregular, but the indentation in the outline of the holotype seems to be a result of breakage rather than original form. Although the sclerite in fig. 11 has the fine perforations of the holotype, it is questionably assigned to this species because the perforations are more uniform in size and are arranged in straighter rows, and the border of the plate is more regular than that of the type. *T. irregularis* is differentiated from other species in the genus on the basis of the fine and very numerous perforations. *T. mccormacki* most nearly resembles it, but possesses fewer and larger perforations in a more regular arrangement.

THUROHOLIA? sp.
Pl. 125, figs. 18,19

Description.—Small, nearly flat, thin plates resembling the perforate plate form of sclerites, but covered with very fine depressions which in most specimens do not penetrate through the plate. Shape varies from circular to ellipitical to irregular. Depressions are regular in size, about 0.01 mm. or less, numerous and rather close together, but in no recognizable pattern. Border usually smooth.

Dimension.—Diameter, 0.51 mm. and smaller.

Remarks.—These plates are found in considerable numbers along the same surfaces as the accepted sclerites. In composition and general structure they resemble closely the perforate plates. The extremely fine, uniform depressions and the delicate structure differentiate these forms from other sclerites. Their taxonomic position is uncertain: they may represent immature holothurian plates or may belong to some other group of echinoderms.

PETROPEGIA, n. gen.

Diagnosis.—Sclerites in form of large, flat perforate plates of varied outline and characterized by a spinose border. In some forms the spines are developed only peripherally; in others, they are recognizable as thickened or raised walls for some distance in toward the center of the plate. The general appearance is of a plate strengthened by radial supports.

Perforations vary in size and arrangement; margins between the spines may be smooth or irregular; maximum known length of spines beyond margins, 0.25 mm.

Dimension.—Diameter variable; maximum observed, 2.85 mm.

Type species.—*Petropegia radiata*, n. sp.

Remarks.—The peripheral spines of these plates are so distinctive as to warrant their spearation from *Thuroholia* and placement in a new genus in the family Calclamnidae. The spines can be distinguished from projections of broken perforation walls by their length and their rather smooth outline. The species described include plates that vary in shape and in arrangement of spines.

PETROPEGIA RADIATA, n. sp.
Pl. 126, figs. 22,23

Description.—Very large, flat perforate plates with a somewhat circular outline interrupted by projecting spines which can be traced in toward center of plate as strong radial axes. Spines or axes extend as much as 0.25 mm. beyond the border of the plate, and die out about two-thirds of the way into the center; border between spines irregular. Perforations generally subcircular, varying from 0.07 to 0.15 mm. in diameter, arranged in straight rows having nearly radial pattern. Perforate texture of plate usually coarse.

Dimension.—Greatest diameter of holotype, 2.85 mm.

Types.—Deposited in University of Kentucky, Department of Geology Collection. Holotype No. TC 94.

Remarks.—This species is known from a single, well-preserved specimen and a number of fragments showing the strong axial supports. It is the largest sclerite of the perforate type reported. The structure is so distinctive as clearly to warrant its recognition as a separate species.

PETROPEGIA SPINOSA, n. sp.
Pl. 126, figs. 20,21

Description.—Sclerites in form of flat perforate plates, moderate to large size, of roughly rectangular outline and with spines projecting at the corners and along the sides. Spines identifiable as strong axes extending from some distance within the border and usually projecting beyond it at least twice the diameter of the perforations. Perforations of rather constant diameter, about 0.06 mm., subcircular to hexagonal in outline, arranged in a regular pattern of straight rows that tend to parallel the diagonals marked by the corner spines. Overall dimensions uncertain; some diagonals, including spinose projections, about 1.3 mm.

Dimension.—Greatest diameter of holotype (fig. 21), 1.2 mm.

Types.—Deposited in University of Kentucky, Department of Geology Collection. Holotype No. TC 95.

Remarks.—The species is represented by several specimens, but unfortunately none

is complete. Some of the projecting spines of the holotype, fig. 21, were broken in the attempt to free it from the matrix; observations pertaining to the general outline were made prior to the breaking. *P. spinosa* differs from *P. radiata* in its smaller size, generally rectangular form, and fewer spines in more regular arrangement.

Family ETHERIDGELLIDAE Frizzell & Exline, 1955

Genus ETHERIDGELLA Croneis, 1932

Diagnosis.—Sclerites in form of imperforate disks, concavo- or plano-convex, with low rounded spire-like rise (pseudospire) on the convex side; outline generally circular to subcircular; surfaces covered by alternating depressions and nodes of roughly polygonal outline.

It is proposed here that the generic description be expanded to include biconvex forms of the same general characteristics.

Type species.—*Etheridgella porosa* Croneis.

ETHERIDGELLA BICONVEXA, n. sp.
Pl. 126, figs. 10–12

Imperforate disks or buttons, CRONEIS & MCCORMACK, 1932, p. 145, pl. 21, figs. 46, 51.

Description.—Sclerites in form of thick imperforate disks or buttons, circular to elliptical in outline, slightly to strongly biconvex, one surface tending to be more convex than the other; more flattened or disk-like specimens have a narrow, smooth equatorial flange. Surfaces of buttons pitted: on larger specimens the "upper," more convex surface has better developed and somewhat more regularly shaped pits; on smaller specimens, depressions appear to be fine textured, generally less well developed, and of no particular shape.

Dimensions.—Diameter of holotype (fig. 12), 0.55 mm. Range of diameter of specimens studied varies from 0.2 mm. to 0.55 mm.

Types.—Deposited in University of Kentucky, Department of Geology Collection. Holotype No. TC 97.

Remarks.—*E. biconvexa* differs from the type species mainly in cross-section shape. As can be seen from the figures, the forms in this species, although all biconvex, include some that are relatively greater in diameter and more flattened, and others that are less in diameter and more round. Perhaps it would be justifiable to separate these forms into two species.

Although the holothurian affinities of these disks and buttons are still open to question, the surface markings, general outline, and association support a holothurian orgin.

Family ACHISTRIDAE Frizzell & Exline 1955

Genus ACHISTRUM Etheridge, emend. Frizzell & Exline 1955

Diagnosis.—Sclerites in form of hooks, with component parts designated eye, shank and spear. Species vary in shape and position of eye; in length, cross-section shape, and taper of shank; and in curvature of spear. Length ranges from 0.20 to 1.25 mm.

ACHISTRUM BROWNWOODENSIS? (Croneis)
Pl. 126, fig. 8

Description.—Sclerite in form of hook; thin, elliptical; long straight shank curving at base to form spear. Eye small, normal to plane of spear, circular and centered to axis of shank; about 0.18 mm. wide, with small, circular perforation about 0.05 mm. wide. Length reported to range from 0.72 to 0.90 mm.

Remarks.—Fragment of sclerite identified as *A. brownwoodensis* mainly on basis of centered circular eye and portion of apparently straight, non-tapering shank.

ACHISTRUM LUDWIGI (Croneis)
Pl. 126, figs. 1,2

Description.—Sclerites in form of hooks; shank long, thin, slightly curved, tapering toward eye, elliptical in cross section; spear short and sharply curved; eye rather large, asymmetrical and slightly inclined toward spear in plane of spear; eye loop appears as tapering extension of shank, becoming thinner along recurved side; eye perforation large, elliptical. Outside diameter of loop on specimens examined ranges from 0.18 to 0.22 mm.

Dimensions.—Length of fig. 1, 1.22 mm.; fig. 2, 0.68 mm.

Remarks.—The nearly complete specimen shown in fig. 1 is as long as the maximum length given for incomplete forms of the previously published descriptions (0.97 to 1.22 mm.). Although the structure of the eye loop is uniform in the specimens found in the Kendrick, it is not indicated as diagnostic in previous descriptions.

ACHISTRUM MONOCHORDATA? Hodson, Harris, & Lewison
Pl. 126, figs. 3–7

Description.—Sclerites in form of hooks. Shank straight, rather heavy, 0.06 to 0.08 mm. in diameter, circular in cross section. Spear unknown. Eye large and asymmetrical, about 0.18 mm. outside diameter; loop somewhat elliptical, divided by a crossbar; position and orientation of crossbar varies from almost midpoint to so close to the side that is only an incipient divider.

Dimensions.—Length of forms figured, 0.53 to 0.84 mm. Reported length of incomplete holotype, about 0.61 mm.

Remarks.—The tentative identification of *A. monochordata*—originally described from the Oxfordian of Yorkshire—among the Kendrick sclerites has raised some problems. This species is differentiated entirely on the basis of a crossbar within the eye loop. Our specimens generally fit the definition of *A. bartensteini* Frizzell & Exline from the Lias of Germany except that the eye has a dividing crossbar rather than the "thorn-like process" described in *A. bartensteini.*

As pointed out in the description of *A. monochordata* (Hodson, *et al.*, 1956, p. 341), the position of the crossbar is variable, and in many specimens it is almost fused with the eye rim. The Kendrick forms exemplify this variation: in some, the eye is almost equally divided by the crossbar; in others, the bar is displaced almost to the rim and on the rim side only an incipient perforation or dimple is present.

When the crossbar is well separated laterally from the rim it can be seen to flare rather strongly toward one end. If this flaring and thickened end were the only part remaining after the rest of the crossbar had been broken out or covered by a matrix-filling of the eye perforation, a tooth-like process would seem to be present. Further study may show that *A. monochordata* and *A. bartensteini* belong to the same species or that the presence or absence of a dividing process within the eye is not a suitable characteristic for differentiation into separate form species.

ACHISTRUM NICHOLSONI? Etheridge
Pl. 126, fig. 9

Description.—Sclerite in form of a hook; shaft long, straight, circular in cross section; hook portion missing, and taper of shaft not recognizable; eye large, nearly centered to shaft in plane of shaft; eye perforation large, elliptical to triangular; eye loop thickened on upper border.

Dimension.—Length, 0.62 mm.

Remarks.—The specimen figured is longer than the average length (0.58 mm.) reported for this species. Because of the absence of taper of the shaft and the slightly off-center position of the eye, the identity of the specimen is questionable.

Family THEELIDAE Frizzell & Exline, 1955
Genus THEELIA Schlumberger, 1890

Diagnosis.—Sclerites in form of wheels with 6 to 10 spokes, commonly 6 or 7; rim curved upward and inward to plane of wheel; usually denticulate on inner margin; central portion solid or imperforate, sometimes flat, depressed or with a conical button or other ornamentation, but never with cylindrical raised hub. Diameter ranges from about 0.05 to 0.7 mm.

Type species.—*Theelia undulata* (Schlumberger).

THEELIA HEXACNEME, n. sp.
Pl. 126, fig. 3

Description.—Sclerite a six-spoked wheel, small, generally circular to slightly hexagonal in outline, with edge scalloped; scallops opposite interspoke area. Spokes wide, straight sided, merging toward center of wheel to form a solid area covering one-third the total diameter; each spoke curves rather sharply upward toward rim; interspoke space triangular, with outer edge slightly curved. At center juncture, or hub, each spoke has a small knob, or button; center area proper is smooth and slightly depressed. No denticulation observed along

either rim or spoke surfaces; upper surface unknown.

Dimension.—Diameter, 0.17 mm.

Remarks.—***Theelia hexacneme***, n. sp., is most similar to ***Theelia ingens*** (Joshua). It differs in its smaller size, in the presence of knobs in the central area, and in its narrower outer rim. Although the genus definition includes denticulation, its absence or lack of recognition in this specimen is not considered exclusive, since it is similarly unknown in other species ascribed to the genus, *e.g.*, *T. ingens* (Joshua) and *T. rotula* (Egger).

Genus PROTOCAUDINA Croneis, 1932

Diagnosis.—Sclerites in form of wheels of circular to subcircular outline, with 8 to 10 short spokes separated by small, triangular to elliptical openings. Central portion large with four perforations in varied arrangements. Rim inclined to plane of wheel and frequently scalloped; dentations often present. Diameter from 0.07 to 0.55 mm. in reported specimens.

Type species.—*Protocaudina traquairii* (Etheridge).

PROTOCAUDINA KANSASENSIS (Hanna)
Pl. 126, figs. 14–17

Description.—Sclerites in form of wheels, circular to elliptical in outline; rim inclined to plane of wheel, and upper surface of rim scalloped; ten short spokes separated by oval to slightly triangular openings wider than spokes. Central portion large, with four subtriangular perforations arranged in an elliptical pattern, one pair close together and the other more widely spaced; all well separated from outer spoke area. Lower surface gently convex with smooth cross-section profile; upper surface sharply rimmed, slightly concave, with area of inner perforations commonly more sharply depressed.

Dimensions.—Diameter of specimens figured, 0.15 to 0.27 mm. Diameter reported for species, 0.25 to 0.52 mm.

Remarks.—This is the most common wheel-type sclerite in the fauna. The specimens vary from the published descriptions only in their smaller size.

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JOURNAL OF PALEONTOLOGY, V. 32, NO. 5, P. 970–976, PL. 127, 2 TEXT-FIGS, SEPTEMBER 1958

MERAMECIAN (MISSISSIPPIAN) ENDOTHYRID FAUNA FROM THE ARROYO PEÑASCO FORMATION, NORTHERN AND CENTRAL NEW MEXICO

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ABSTRACT—An endothyrid fauna of Meramecian age is described and illustrated from the Arroyo Peñasco formation of northern central New Mexico. This fauna and the enclosing rocks represent a western extension of the Meramecian episea of southwestern Kansas, western Oklahoma and northwestern Texas. *Endothyra prodigiosa* new species, *Endothyra macra* Zeller, and several unnamed species of *Plectogyra* and *Endothyra* are described and illustrated. Comparison is made with the endothyrids of the Leadville limestone (Lower Osagian) of the San Juan Mountains, Colorado. Its diagnostic microfossil *Granuliferella* aff. *granulosa* Zeller is described and illustrated. *Plectogyra* sp. from the Kelly formation (Keokuk) of west-central New Mexico is also described and illustrated.

ACKNOWLEDGMENTS

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INTRODUCTION

The limestones and dolomitic limestones of the Meramecian Arroyo Peñasco formation are exposed as isolated pre-Pennsylvanian erosional outliers in many of the mountain ranges of central and northern New Mexico. It is from 10 to 140 feet thick and rests on a peneplained surface of Precambrian igneous and metamorphic rocks. It is unconformably overlain by the basal clastics of the Pennsylvanian System. The Arroyo Peñasco formation at many localities shows extensive evidence of pre-Pennsylvanian karsting. The Arroyo Peñasco formation was once considered to be the lower limestone member of the Sandia formation of Pennsylvanian age (Read & Andrews, 1944). This dating was followed, due to the lack of paleontologic evidence, by Read *et al.* (1944), Kelley & Wood (1946), Northrop *et al.* (1946), Wood & Northrop (1946) and Read & Wood (1947). Several of these authors suggested that the lower limestone member, because of stratigraphic position and lithologic similarity to the Leadville limestone, might represent a pre-Pennsylvanian erosional remnant of lower Mississippian rock. Henbest (1946, p. 760) claimed to have found *Endothyra baileyi* (Hall) in the Leadville limestone of the San Juan Mountains, Colorado and in the lower limestone member of the Sandia formation in the southern Sangre de Cristo Mountains, New Mexico. On the basis of this foraminifer, which he did not illustrate, and lithic similarity he extended the San Juan facies of the Leadville limestone 200 miles southwestward. Armstrong (1955) collected a small megafossil fauna and a number of endothyrid foraminifera from various stratigraphic horizons of the lower limestone of the Sandia formation in northern and central New Mexico. He judged the microfauna of the lower limestone of the Sandia formation to be of Meramec age, and named it the Arroyo Peñasco formation. He considered it to be a pre-Pennsylvanian erosional remnant of a thin, but once extensive, sheet of Meramecian limestone which stretched westward into northern and central New Mexico from western Kansas, Oklahoma and northwestern Texas. Fitzsimmons, Armstrong & Gordon (1956) published a faunal list of megascopic fossils collected from the highest 20 to 30 feet of the Arroyo Peñasco formation from Peñasco

Canyon, Nacimiento Mountains and the northern end of the San Pedro Mountains. Mackenzie Gordon and Helen Duncan of the United States Geological Survey identified the fossils as indicative of St. Louis time (Meramecian). Read (1956, p. 17) thought the Arroyo Peñasco formation of the southeastern Sangre de Cristo Mountains was equivalent to the Upper Devonian and Lower Mississippian strata of the San Juan Mountains, Colorado. He believed the basal silty and sandy beds of the Arroyo Peñasco formation represented the Upper Devonian Elbert formation of the San Juan Mountains, Colorado. Above the basal beds is a sequence of medium bedded limestones he identified as the Upper Devonian Ouray formation. This in turn according to Read was brecciated in its higher portions due to the development of a karst topography on its surface prior to the deposition of still younger limestone strata which he correlated with the Leadville limestone of Lower Mississippian age. These are in turn overlain unconformably by basal Pennsylvanian clastics. Read (1956, p. 17) admitted that paleontologic evidence was lacking for his correlation, but justified it on lithologic similarities and stratigraphic position.

PALEONTOLOGIC NATURE OF THE ARROYO PEÑASCO FORMATION

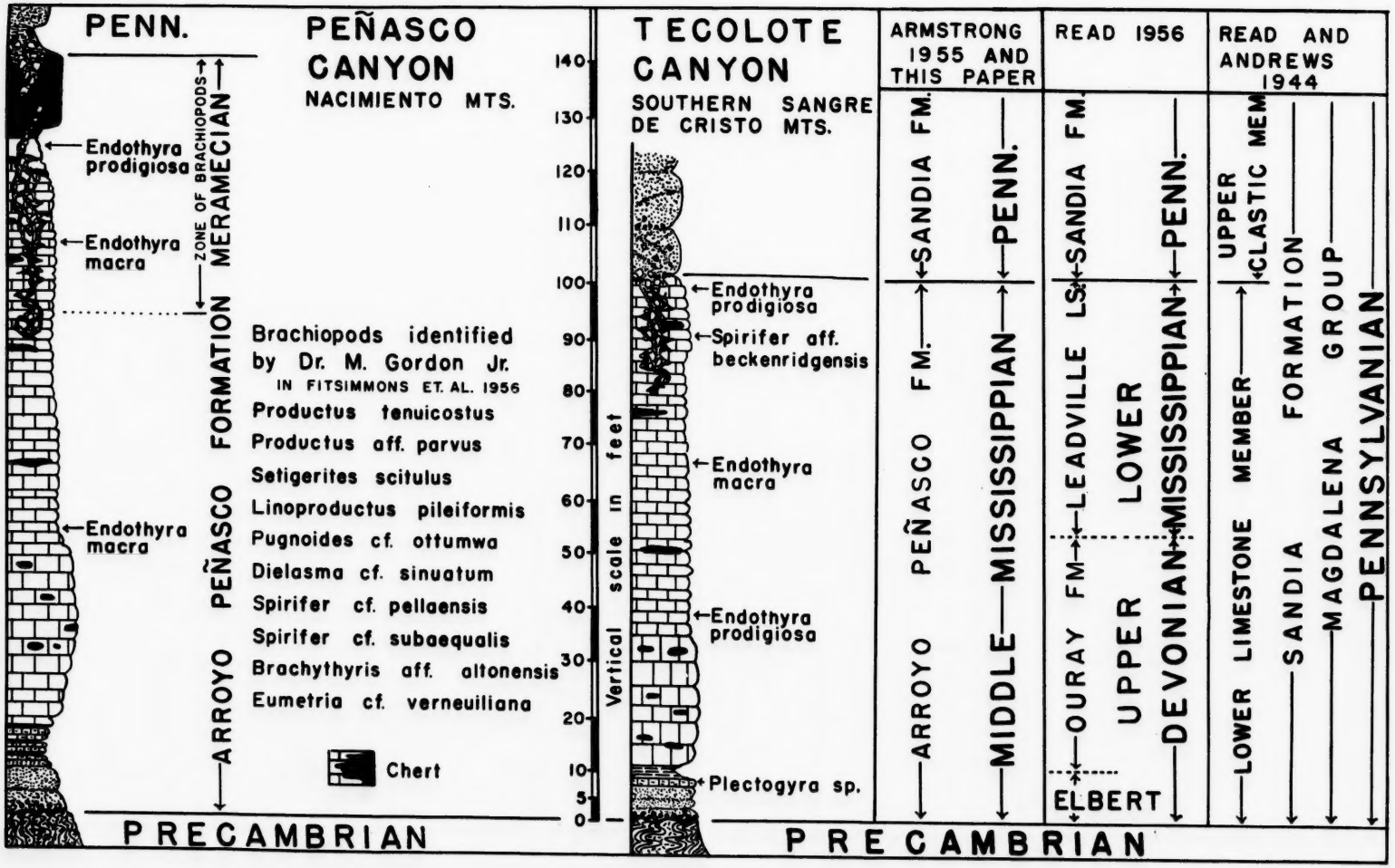
Megascopic fossils are extremely rare in the Arroyo Peñasco formation. They are present at a few localities however and occur almost exclusively at a horizon a hundred feet or more above the peneplain surface. The vast majority of such fossils have come from Peñasco Canyon, Nacimiento Mountains. This fauna was reported by Fitzsimmons, Armstrong & Gordon (1956). The rather extensive linear outcrops of the Arroyo Peñasco formation in the Sangre de Cristo Mountains have yielded only a handful of fossils. Several colonies of *Lithostrotion* sp. were found in Rio Grande de Rancho Canyon, southeast of Taos, and a number of *Spirifer* sp. aff. *S. beckenridgensis* Weller, from Tecolote Canyon, southwest of Las Vegas.

Endothyrids are sufficiently abundant in the Arroyo Peñasco formation and distributed over a wide enough area to offer a substantial basis for regional correlation. Although a number of species of *Plectogyra* and *Endothyra* are present, only one species of each genus is abundant enough to be readily readily used for this purpose. *Endothyra prodigiosa*, n. sp., is present in most of the pure limestone of the Arroyo Peñasco formation in northern and central New Mexico. Both size and contour indicate the Meramecian stage of endothyrid evolution.

A rather rare unidentified *Plectogyra* is of value in stratigraphic correlations because of its wide geographic distribution. Sufficient number of properly oriented sections could not be obtained for specific identification. In its larger size (0.6 to 0.7 mm. in diameter), this *Plectogyra* is definitely of Meramecian aspect, and contrasts strongly with the known Osagian species, all of which are smaller in size. It compares very closely with Zeller's (1951, pl. 4, figs. 4,6,7) *Plectogyra* sp. from the Ste. Genevieve limestone, Ste. Genevieve, Missouri. This *Plectogyra* occurs sporadically in the basal 10 to 20 feet of argillaceous limestones in the Arroyo Peñasco formation of the southeastern side of the Sangre de Cristo Mountains from Rincon Range, north of Mora, New Mexico to Tecolote Canyon, southwest of Las Vegas, New Mexico. So far this *Plectogyra* has not been observed in the Nacimiento, San Pedro or Sandia Mountains section, nor has it been found in the higher limestones.

Sufficient endothyrids have been found throughout the Arroyo Peñasco formation in the southeastern Sangre de Cristo Mountains to state without hesitation that the entire formation here is of Meramec age.

The Arroyo Peñasco formation in the Sandia, Nacimiento and San Pedro Mountains does not present such a simple picture. The lower 30 to 35 feet of limestone have yielded no fossils. Both microfossils and megafossils in the remainder of the sequence indicate Meramecian time. No distinct difference in lithologies or any noted sign of a hiatus was observed between the unfossiliferous beds and the endothyrid bearing horizons. The unfossiliferous strata are lithologically similar to the same stratigraphic horizons which bear endothyrids in in the Sangre de Cristo Mountains. But these barren beds, as well as the Meramecian endothyrid-bearing higher zones resemble lithologically the fossiliferous Lower Missis-



TEXT-FIG. 1—Typical examples of the Arroyo Peñasco formation, illustrating the terminology and age assignment used by various authors.

sippian Leadville limestone of the San Juan Mountains, Colorado.

As has been previously cited, many authors have felt the strata involved in the Arroyo Peñasco were an extension of the Leadville limestone of southwestern Colorado. In an effort to ascertain the stratigraphic relationship of the Leadville limestone to the Arroyo Peñasco formation, the author collected megafossils and stratigraphic samples from the Leadville limestone at Rockwood Quarry and at Piedra River, San Juan Mountains, Colorado. The Leadville limestone fauna, as was pointed out by Girty (1903), is characterized by *Spirifer centronatus* Winchell *sensu stricto*. The Leadville endothyrids belong to two genera, *Grauliferella* Zeller and *Plectogyra* Zeller. The *Plectogyra* are about 0.5 mm. in diameter, very rare, and compare to forms described by Zeller (1957) from the lower Osagian of the Cordillerian geosyncline. *Granuliferella* aff. *granulose* Zeller is abundant throughout the Leadville limestone. Zeller (1957) found that the genus *Granuliferella* is restricted to the Cordillerian region of the United States and is particularly characteristic of Kinderhookian and lower Osagian limestones.

Eumetria verneuiliana (Hall) is the only species so far found to occur in both the Leadville limestone and the Arroyo Peñasco formation. The presence of this distinctly Meramecian fossil of the midcontinent region with otherwise lower Osagian Leadville fauna was commented on by Girty (1903, p. 305). Neither Leadville limestone type of *Plectogyra* or *Granuliferella* has ever been observed in the Arroyo Peñasco formation.

Although the Leadville limestone and the Arroyo Peñasco formation occupy similar positions in the stratigraphic sequence and have similar lithofacies, the faunas indicate quite different age assignments and paleogeographic provinces. The Leadville limestone seems to be in age and geography a part of the early Mississippian record of the Cordilleran province, an extension of the Madison limestone complex, whereas the Arroyo Peñasco formation appears to have been deposited in a southwestward extension of the midcontinent episea of Meramecian time, via Kansas, Oklahoma and northwestern Texas.

SYSTEMATIC PALEONTOLOGY

Genus GRANULIFERELLA E. J. Zeller 1957

GRANULIFERELLA sp. aff. G. GRANULOSA Zeller

Pl. 127, figs. 13–14

Granuliferella granulosa Zeller, E. J., 1957, p. 695, pl. 77 figs. 1,7,8,14,19, 20; pl. 78, fig. 2; pl. 79, figs. 3,4,5,20,21,22; pl. 81, figs. 4,5,7,8,10; pl. 82, figs. 6,7.

The shell is discoidal, involute, and apparently more umbilicated on one side than on the other. The chambers are large in proportion to the size of the shell and are swollen between the sutures. The septa are short and anteriorly directed. The aperture was not observed. In a number of the specimens there seems to be present the specific trait of *G. granulosa*, a marked thickening of the walls of the chambers in the last volution. Secondary deposits were not observed. The coiling is distinctly plectogyroid. The proloculus was indistinct in all the specimens observed. The diameter of the adult shell is from 0.3 to 0.4 mm.

Remarks.—Of the described species of *Granuliferella*, the Leadville forms most closely resemble Zeller's (1957, p. 695) specimens of *G. granulosa* from the Madison limestone and its stratigraphic equivalents in Montana, Wyoming and Utah. Because of the poor state of preservation and the lack of properly oriented section, definite specific identification cannot be made.

Horizons.—*G.* aff. *granulosa* was found throughout the Leadville limestone from its base on the *Cyrtospirifer*-bearing, Upper Devonian, Ouray formation to its contact with the Pennsylvanian, Molas formation at both Rockwood Quarry and Piedra River in the San Juan Mountains, Colorado.

Genus ENDOTHYRA Brown 1843

ENDOTHYRA PRODIGIOSA, n. sp.

Pl. 127, figs. 1–3,5–8

The shell is discoidal, involute; and the chambers are only slightly swollen between sutures. Coiling is planispiral. Septa show anterior direction. The proloculus is 40 to 50 microns in diameter. A prominent hamulus or hook is present on the floor of the final chamber. On the floor in the next to final chamber a tumulus or little hill is present. Septal count from the first to the fourth

TEXT-FIG. 2—Index map of the area under consideration, showing the location of measured section, their thickness and the characteristic endothyrid. Lithostratigraphic details of each section can be found in Armstrong (1955).

volution is 8, 9, 11, 12 respectively. The coiling shows a medium rate of expansion. Adult shells average from 0.8 to 1.1 mm. in diameter.

Remarks.—*Endothyra prodigiosa* differs from *E. symmetrica* (in which the average shell is 0.4 mm. in diameter (Zeller, 1957, p. 701)) by its much larger size. *E. prodigiosa* differs from *E. macra* Zeller, again by its much larger size and more regular rate of expansion. *E. prodigiosa* resembles, except for its slightly larger size, higher septal count and slower rate of expansion, Zeller's (1951, pl. 4, figs. 3,5,14) *Endothyra* sp. from the St. Louis and Ste. Genevieve limestones of eastern Missouri.

Horizon.—*E. prodigiosa* occurs throughout most of the microfossiliferous zones in the Arroyo Peñasco formation. It is particularly abundant in the upper fourth of the formation in Peñasco Canyon, Nacimiento Mountains and Tecolete Canyon, Sangre de Cristo Mountains. *E. prodigiosa* occurs within the same limestone and chert horizon at Peñasco Canyon which yielded the Meramecian megafauna reported by Fitzsimmons, Armstrong, & Gordon (1956, p. 1943).

Endothyra macra Zeller
Pl. 127, fig. 4

Endothyra macra Zeller, E. J., 1957, p. 702, pl. 80, figs. 7,14.

The chambers are slightly swollen between sutures. Septa are long and anteriorly directed. The coiling is planispiral. The proloculus appears to be from 10 to 20 microns in diameter. A hannulus or hook is present in the final chamber of most examples. The septal count from the first to the fourth volutions are 6, 8, 9, 11 respectively. The first two volutions of the shell are tightly coiled, the third shows a more rapid expansion, whereas the last volution rapidly expands. Adult shells average 0.5 to 0.6 mm. in diameter.

Remarks.—Zeller (1957, p. 702) states the characteristics of the species are its rather large size (0.6 mm.) and the sharp change in the rate of shell expansion in the third and fourth volutions. The Arroyo Peñasco specimens differ from Zeller's (1957, pl. 80, figs. 7,14) *E. macra* in that the third volutions do not expand quite as rapidly.

Horizon.—*Endothyra macra* occurs sparcely in most of the microfossiliferous zones of the Arroyo Peñasco formation. Zeller (1957, p. 702) reports its occurrence at the top of Brazer formation at Blacksmith Fork Canyon, Utah. *E. macra* according to Zeller (1957, p. 691) is found only in the upper part of the Brazer limestone with a microfauna similar to that present in the Ste. Genevieve limestone of the Mississippi valley.

Genus PLECTOGYRA E. J. Zeller 1950
PLECTOGRYA sp. No. 1
Pl. 127, figs. 9–11

Chambers are slightly swollen between sutures. Septa are of medium length and have an anterior direction. The proloculus is from 20 to 30 microns in diameter. Secondary deposits and aperture were not observed. The coiling is plectogyroid and shows a moderate angle of distortion. Adult shells show four to four and a half volutions. Mature shells are from 0.6 to 0.7 mm. in diameter.

Remarks.—Sufficient oriented specimens of this Plectogyrid could not be obtained for specific identification. Because of its large size and contour, it compares very closely with Zeller's (1951, pl. 4, figs. 4,6,7) examples of *Plectogyra* sp. from the Ste. Genevieve limestone, Ste. Genevieve, Missouri.

Horizon.—It occurs exclusively and rather sporadically in the basal 10 to 20 feet of argillaceous limestones of the Arroyo Peñasco formation in the Sangre de Cristo Mountains from north of Mora to Pecos Canyon.

PLECTOGYRA sp. No. 2
Pl. 127, fig. 17

The shell is from 0.4 to 0.5 mm. in diameter. The coiling is plectogyroid; total angular distortion is moderate. The last two chambers are collapsed. The septa are anteriorly directed. A hamulus or hook is present in the last chamber. This same structure is partially reabsorbed in the next to last chamber. The aperture is low and is situated at the base of the apertural face. The tumulus does not appear to show positive evidence of reabsorption. Adult shells show three to four volutions.

Remarks.—Zeller (1951, p. 12) observed

in the endothyrids of the Mississippi Valley that the collapse of the final chambers is a specific trait of Keokuk forms and that this characteristic was not found in horizons above or below the Keokuk. The New Mexico form occurs in a horizon carrying a rich blastoid and brachiopod fauna typical of a Keokuk age.

Horizon.—The specimen was found in the upper half of the Kelly formation of Keokuk age, on the crest of the Magdalena Mountains, west-central New Mexico.

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MANUSCRIPT RECEIVED MARCH 18, 1958.

EXPLANATION OF PLATE 127

All illustrations on this plate are unretouched ×50

FIGS. *1–3,5–8—Endothyra prodigiosa* Armstrong. *1,2*, horizontal axial section, *2*, holotype; *3*, vertical section; *5–8*, oblique vertical sections. All are from the Arroyo Peñasco formation. *1,2,5–8* from Tecolote Canyon, Sangre de Cristo Mountains. *3*, from Peñasco Canyon, Nacimiento Mountains.

4—Endothyra macra E. J. Zeller. Horizontal axial section. Arroyo Peñasco formation, Peñasco Canyon, Nacimiento Mountains.

9–11—Plectogyra sp. no. 1. 9, oblique vertical section. *10–11*, oblique horizontal sections. All from Arroyo Peñasco formation. *9,11*, from Lujan Canyon, Rincon Range, Sangre de Cristo Mountains. *10*, Gallinas Canyon, Sangre de Cristo Mountains.

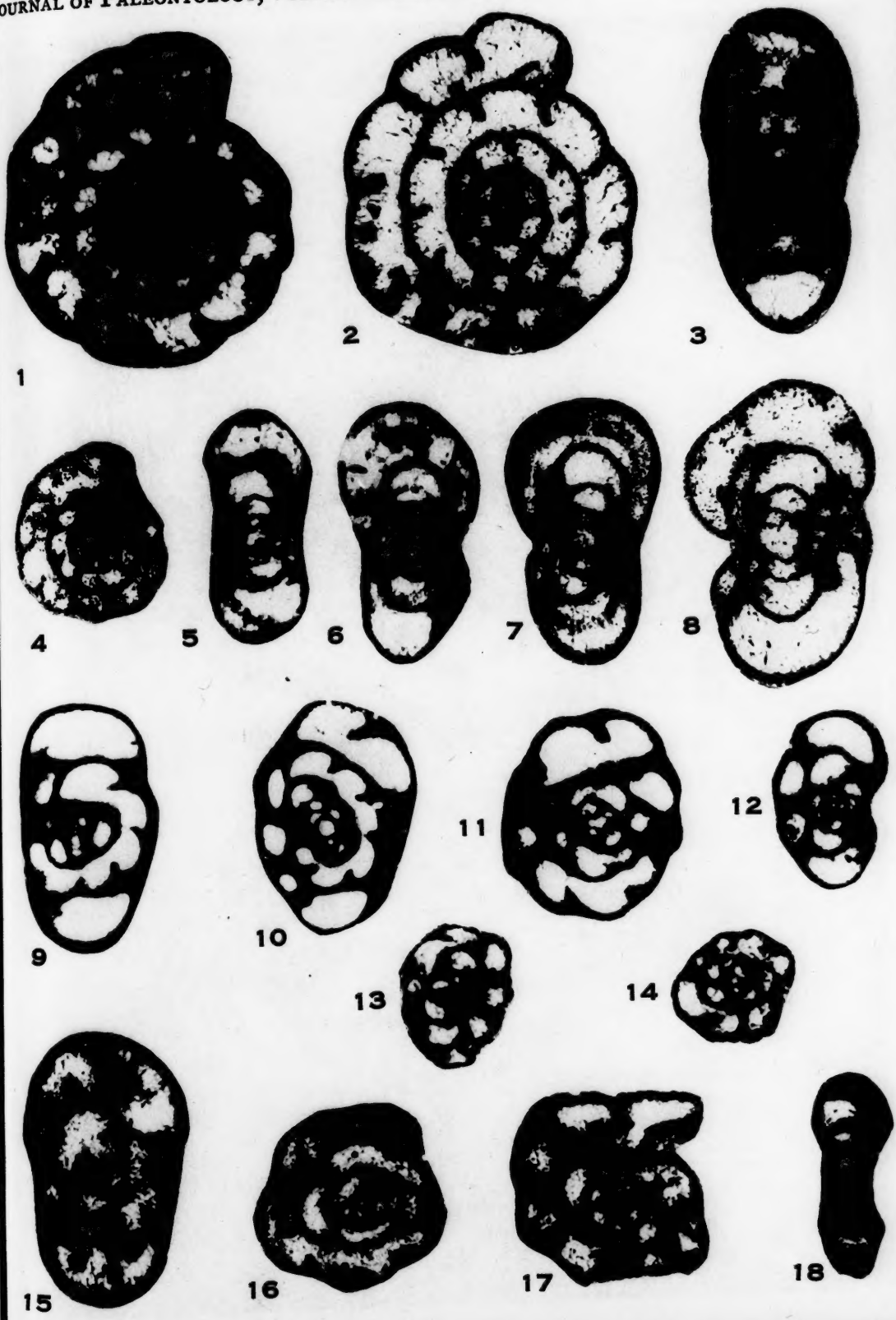
12—Plectogyra sp. Oblique vertical section. Arroyo Peñasco formation, San Pedro Mountains.

13–14—Granuliferella aff. *granulosa* E. J. Zeller. Oblique sections. *13*, Rockwood Quarry. *14*, Piedra River Canyon, Leadville limestone, San Juan Mountains, Colorado.

15–16—Plectogyra sp. *15*, oblique vertical section. *16*, oblique horizontal section. Arroyo Peñasco formation, San Pedro Mountains.

17—Plectogyra sp. no. 2. Horizontal section. Kelly formation of Keokuk age, crest of Magdalena Mountains.

18—Plectogyra sp. Vertical section. Rockwood Quarry, Leadville limestone, San Juan Mountains, Colorado.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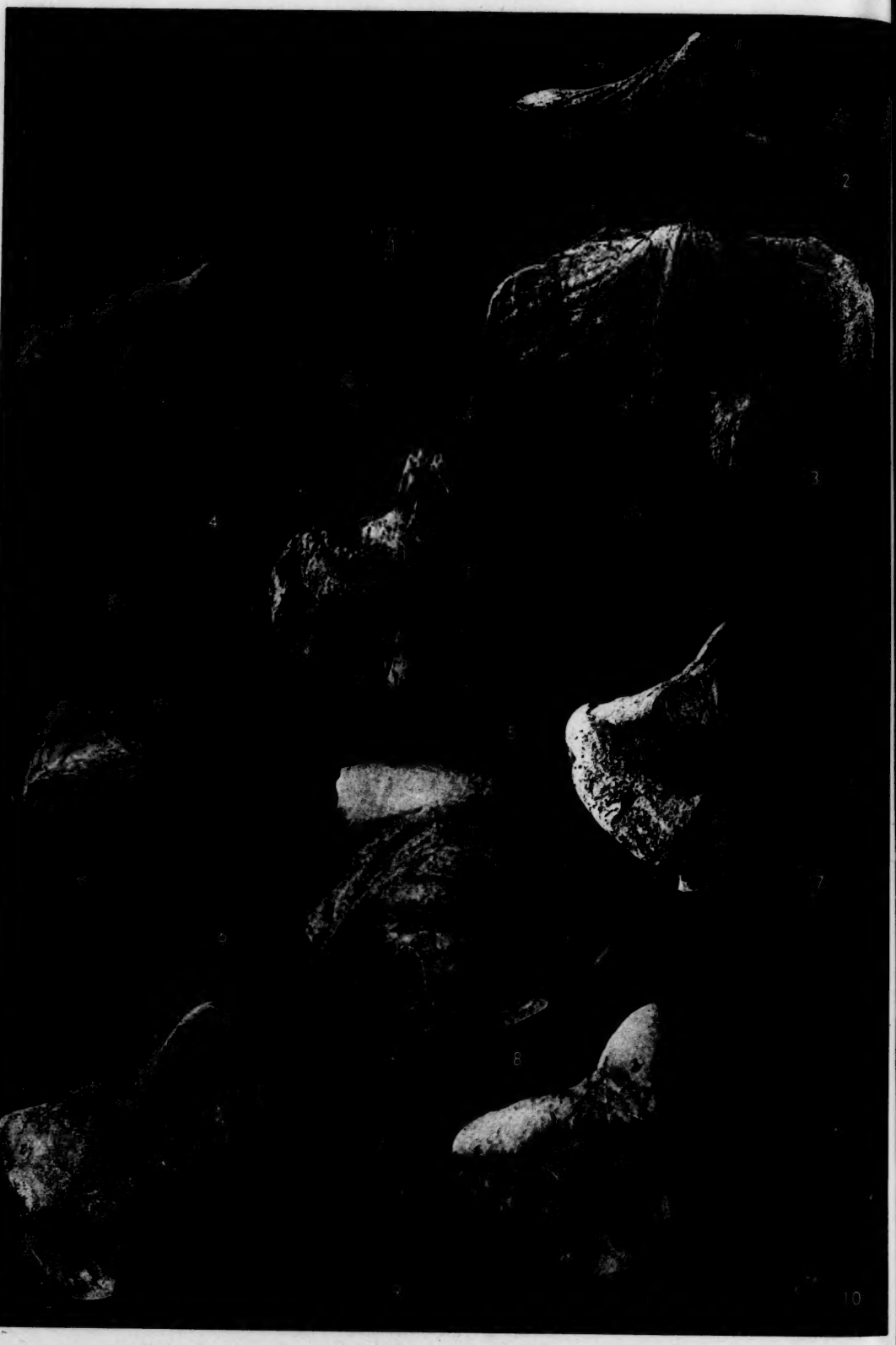

JOURNAL OF PALEONTOLOGY, V. 32, NO. 5, P. 977–980, PL. 128, SEPTEMBER 1958

TWO NEW INVERTEBRATES FROM THE MISSISSIPPIAN OF NEVADA*

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ABSTRACT—A gigantic spiriferoid brachiopod from the Diamond Peak formation (U. Miss.) is named *Dimegalasma eurekensis*. It is larger than other species of this genus, has four to five costae on each side of the large fold, and a less cyrtinoid pedicle beak than found on other species. Previously known species of this genus are restricted to Keokuk and Burlington limestones of the Midcontinent Region.

A gyroconic nautiloid from the upper Mississippian is referred to Flower's Order Rutoceratida. *Elkoceras volborthi*, n. gen. and n. sp., possesses a tightly coiled neanic stage and gyroconic adult stage, subtrigonal whorl profile and alternating nodes at the ventral margin. Possible relationships within the Rutoceratida are discussed.

INTRODUCTION

IN THE fall and winter months of 1956 two interesting invertebrates were collected from the upper Mississippian rocks in Nevada. Both appear to be widely distributed, but of restricted range and numbers of specimens. Their sparsity will perhaps prevent them from attaining maximum utilization as index fossils, but nevertheless, at this time, they appear to have value as horizon markers. Neither invertebrate represents a discovery on the part of the authors, for the brachiopod has been mentioned in a faunal list, and the cephalopod, although undescribed, had been collected previously. The unusual size of the brachiopod and the rarity of gyroconic nautiloids have prompted the authors to prepare this notice and to provide these fossil forms with valid nomenclature.

We acknowledge the help and interest in these forms received from Mackenzie Gordon, Jr., and Ralph L. Langenheim, Jr. The Research Committee of the University of Nevada contributed a grant-in-aid to assist in preparing the illustrations. The Nevada Bureau of Mines provided field expenses.

* Published with the permission of the Director, Nevada Bureau of Mines.

SYSTEMATIC DESCRIPTIONS

Phylum BRACHIOPODA
Order SPIRIFERIDA
Genus DIMEGALASMA Cooper
DIMEGALASMA EUREKENSIS, n. sp.
Pl. 128, figs. 2–10

Gigantic, spiriferoid in outline and profile with smooth fold and sulcus. Flanks with four or five distinct costae. Pedicle interior with long, strong dental plates. Delthyrium partially covered by a flat delthyrial plate. Brachial interior with short, low median septum supporting a concave hinge plate. Growth lines visible on smooth fold, less so on sulcus. Pedicle beak slightly but not conspicuously cyrtinoid. Length/width ratio approximately 0.842.

Discussion.—The specimens here described

EXPLANATION OF PLATE 128

FIG. *1*—*Elkoceras volborthi*, n. gen. and sp. View of the holotype, Mackay School of Mines Museum 918, ×1.

2–10—*Dimegalasma eurekensis*, n. sp. *2,3*, anterior and dorsal view of a compressed specimen with six costae on either side of the fold. Mackay School of Mines Museum 919, ×¾. *4–7*, lateral, cardinal, anterior and dorsal view of the paratype showing robust development. Mackay School of Mines Museum 920, ×¾. *8–10*, lateral, cardinal and anterior views of the holotype, U.S.N.M. 136134, ×¾.

were found in the fall of 1956 in the upper Mississippian Diamond Peak formation near Eureka, Nevada. Their tremendous size created immediate interest. The collecting site is the Carbon Ridge locality described by Nolan, Meriam, & Williams (1956, p. 64) about nine miles south of Eureka in section 31, T. 18 N., R. 54 E., M.D.B.M. At Carbon Ridge the Diamond Peak formation is a dark-gray, medium to very coarsely crystalline limestone. The beds dip approximately 80° to the southeast and are succeeded by Wolfcampian deposits. The underlying White Pine shale contact is concealed by Quaternary alluvium. The specimens are found in a single horizon occurring in a fault block approximately 500 feet in length.

Reference to Nolan, Merriam, & Williams (1956, p. 61) showed these large specimens had been collected previously and listed as *Dimegalasma* sp. undet. Insofar as we can determine, *D. neglectum* (Hall) and *D. plenum* (Hall) are the only species heretofore assigned to this genus.

The short median septum, strong dental plates, the flat delthyrial plate partially covering the delthyrium, and the spiriferoid shape firmly establish assignment to *Dimegalasma.*

Dimensions of the type specimens (in cm.) and comparisons with *D. neglectum* and *D. plenum* are pesented below.

Specimen	Width	Length	Height	L/W Ratio
Holotype	9.77	8.40 (est.)	6.50	.870
Paratype	9.40	8.20	6.42	.872
D. neglectum[1]	5.11	4.17	3.00	.816
D. plenum[2]	6.92	5.93	5.56	.857

[1] Based on illustration by G. A. Cooper in Shimer & Shrock.

[2] Based on illustrations by J. Hall in Iowa G.S., v. 1, pt. 2.

Apart from the extreme size of this species, the next most noteworthy aspect is the height, which lends a massive, robust aspect to the shell. In fact, these forms are so robust that they weigh slightly over a pound each, even with some portion abraded. The costae are four or five in number on each side of the fold. They are easily visible, but are not nearly as conspicuous as those of *D. neglectum.*

In plate 128, figures 2 and 3 show a specimen with six costae which appears to be unique. Four to five costae are visible on each side of the sulcus of the pedicle valve, but they are not as strongly impressed.

The Nevada material is fairly well preserved, with shell substance clearly visible on all specimens. However, there has been abrasion and loss of shell material in all specimens, particularly in the anterior portion of the fold and the cyrtinoid pedicle beak. These imperfections have been valuable in that they permit confirmation of the important interior structures.

The new species differs from *D. neglectum* (Hall) in its greater size, and in having four costae on each side of the fold instead of six seen on *D. neglectum.* It also has a greater length/width ratio and a less cyrtinoid pedicle beak. This species resembles *D. plenum* (Hall) more closely, in overall appearance than it does *D. neglectum,* but still may be easily distinguished by its greater size, greater width, less profound sulcus, and especially, by the four flanking costae, as compared to twenty in *D. plenum.*

In addition to its occurrence at Carbon Ridge in Eureka County, specimens of *D. eurekensis* are reported from the well-known Mississippian White Pine shale quarry five miles north of Elko, Nevada, along state route 11, and from the White Pine shale in the Pequop Mountains. R. L. Langenheim, Jr. kindly loaned a specimen (UCMP 12042) from this locality. It differs from our specimen figured as number 2–3, only in having five costae. In the eastern side of the Pine Valley Quadrangle in the Pinon Range, Fred Smith, of the U. S. Geological Survey, found several specimens which are in the Survey's collection at Menlo Park, California. These specimens are all external molds, but are definitely referable to *D. eurekensis.*

The discovery of *Dimegalasma* in the Cordilleran geosyncline has shown this genus to possess a greater lateral and vertical range than had previously been suspected. *D. neglectum* is restricted to the middle Osagean Keokuk limestone of Iowa, Missouri, Oklahoma, Illinois, Kentucky, and Alabama. *D. plenum* is restricted to the underlying Burlington limestone. *D. eurekensis* is found at its type locality in association with

Moorfieldella eurekensis (Walcott), *Nudirostra carboniferum* (Girty), *Syringothyris "carteri"* (Hall), *Diaphragmus* sp. and *Gigantoproductus* sp. Nolan, Merriam, & Williams (1956, p. 61) consider these forms to indicate upper Mississippian (Chesterian) age. Mackenzie Gordon, Jr. is quoted on the same page as believing firmly that two nautiloids, *Cravenoceratoides* sp. and *Tylonautilus* sp., collected from the type locality of the Diamond Peak formation several miles north, indicate a Chesterian age for these sediments.

The holotype is designated as specimen No. 136134 in the U. S. National Museum.

Phylum MOLLUSCA
Class CEPHALOPODA
Sublcass NAUTILOIDEA
Order RUTOCERATIDA
Genus ELKOCERAS, n. gen.

Tightly coiled meanic stage followed by a gyrocone adult stage. Whorl profile slightly higher than wide, with broad venter and narrow dorsum. Lateral walls bearing alternating nodes at the ventral angulation beginning with the gyroconic coiling. Shell thin. Sutures and siphuncle not seen.

Type species.—E. volborthi, n. sp.

Discussion.—The group of specimens studied do not resemble established genera in many respects. The taphyroconic neanic stage followed by the gyrocone adult stage is uncommon and seldom as well preserved as in these Nevada specimens.

Although this genus fits rather well in Flower's Order Rutoceratida, the assignment to Hyatt's Family Rutoceratidae is made with less confidence. Flower & Kummel (1950, p. 614) place four families in this order, of which the Rutoceratidae are the most primitive. The Family Tetragonoceratidae Flower at first seemed to be the logical group to which we should assign this genus, which could be described as tetragonal in whorl section having a narrower dorsum than venter. In the present group of shells, however, the dorsum is so narrow that the description subtrigonal is more apt. The two pairs of lateral nodes found in the Tetragonoceratidae are not present here; instead, the nodes are in alternating positions, as in *Tainoceras*. It does not resemble any genus referred to the Tainoceratidae and the loose coiling makes it an unlikely candidate for this family which exhibits the tightest coiling of the order. J. S. Turner (1954, p. 219–220) has deemed it desirable to place another new Mississippian gyronic genus in the Rutoceratidae, although he does so with misgivings. In line with this procedure the new Nevada genus is referred to the same family.

ELKOCERAS VOLBORTHI, n. sp.
Pl. 128, fig. 1

Taphyroconic neanic stage of two or three whorls followed by gyroconic adult whorl of living chamber. Whorl profile subtrigonal, height greater than maximum width which occurs at venter. Prominent alternating nodes at ventral-lateral shoulder beginning on the last taphyroconic whorl. Growth lines perpendicular to direction of growth visible on living chamber. Sutures and siphuncle not seen.

Discussion.—This interesting species is based upon several specimens from two localities in northeastern Nevada. The specimens from the well-known White Pine shale exposure on Nevada highway 11 about five miles north of Elko are pyritized, but without preservation of the interior characteristics. The specimen loaned by R. L. Langenheim, Jr. (UCMP 12043) is an external mold from a limestone horizon in the White Pine shale of the Pequop Mountain Range over fifty miles to the east.

The holotype is pyritized, with one side of the gyroconic whorl crushed. All specimens from the type locality have been crushed in this way. The neanic stages of the holotype were damaged during preparation as the probe pierced the paper-thin early whorls.

Details are generally lacking in the closely coiled stages. Whorls are obscure on all specimens seen, so that their numbers can only be estimated. The sharp angulation between the lateral and ventral faces develops early, being well-marked prior to the gyroconic whorl. Nodes commence at approximately the same growth stage and become more prominent with increasing age. They are not paired, but in alternating positions. On the holotype three nodes occur in the space of 20 mm. near the end of the last

whorl. No ribbing occurs on the lateral walls.

The whorl profile is subtrigonal. The dorsum, prior to crushing, was acutely angular, apparently without any flattening. From this angle the lateral faces flare out with gentle convexity. The nodes are restricted to the lowest quarter of this face. The venter appears to have been gently rounded, and bears no influence of the nodes. The last taphyroconic whorl shows a definitely rounded venter, but that of the gyroconic whorl is not positively established.

Greatest dimension of the holotype is 55.7 mm., with the dimension at right angles being 33.9 mm. Widest portion of the whorl is estimated at 12.0 mm. with the whorl height at the same point estimated at not less than 14.0 mm.

The White Pine shale at this locality is referred to the Osagean series by Dott (1955, p. 2219, 2230). Weller *et al.* (1948, Chart 5) indicate principally a Chesterian age for this formation, although they believe its base lies in the Meramecian. Miller, Downs, & Youngquist (1949, p. 610) consider a certain cephalopod fauna from the "White Pine Shale" of northeastern Nye County to be Meramecian, although Nolan, Merriam, & Williams (1956, p. 61) state the same cephalopod fauna to be considered by "some" as late Chesterian. Accepting any of these interpretations of the age of the White Pine shale, makes *Elkoceras* younger than other members of the family to which it is assigned, although perhaps close in age to Turner's genus *Duerleyoceras* (Visean D_2 zone).

This species is named in honor of Dr. Aleksis von Volborth, mineralogist with the Nevada Mining Analytical Laboratory, under whose mineralogical boot the holotype was found in the field. The holotype is designated as number 918 in the collections of the Univeristy of Nevada.

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ON A NEW PELYCOSAUR FROM THE LOWER PERMIAN OF OKLAHOMA, AND ON THE ORIGIN OF THE FAMILY CASEIDAE[1]

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ABSTRACT—*Colobomycter*, n. gen., a small pelycosaur known from a skull from the lower Permian fissure deposits near Fort Sill, Oklahoma, is closely related to *Eothyris* and shows signs of relationship to the caseids, thus supporting the opinion that the latter are derived from among the eothyridids.

THE most problematical family of pelycosaurian reptiles is probably that of the eothyridids, thought to be ophiacodonts that have paralleled the sphenacodonts in the pattern of the dentition. The following is a report of a new eothyridid that shows features indicative of relationship to the caseids.

The single specimen (Text-fig. 1) of this new pelycosaur consists of the greater part of the right side of the dermal skull roof and the right maxillary dentition, catalogued as C.N.H.M. U.R. 272 in the collection of the Chicago Natural History Museum. I am indebted to Dr. E. C. Olson who informed me of the existence of this interesting specimen, to Dr. R. Zangerl for its loan, and to Mr. L. B. Isham who made the drawings used in this paper.

SYSTEMATICS

A survey of the literature shows that this specimen represents a heretofore undescribed genus and species. A description, by the writer, of a portion of the braincase of another, fairly small pelycosaur from the same deposits has appeared elsewhere (1958), but this braincase is much too large for the pelycosaur described here.

Class REPTILIA
Subclass SYNAPSIDA
Order Pelycosauria
Suborder OPHIACODONTIA
Family EOTHYRIDIDAE
COLOBOMYCTER, n. gen.

Diagnosis.—Small; total length of skull of genoholotype estimated at about 50 mm. Features generally as in *Eothyris*, with the following outstanding differences: Dermal skull roof pitted. Frontal enters orbit. Lacrimal meets jugal. Lacrimal excluded from narial margin.

Genotype.—*Colobomycter pholeter*, new species.

COLOBOMYCTER PHOLETER, new species

Diagnosis.—The same as for the genus (the only species).

Type.—C.N.H.M. U.R. 272.

Horizon and locality.—From a fissure deposit in Arbuckle limestone at the Dolese Brothers limestone quarry, north of Fort Sill, in sec. 31, T. 4 N., R. 11 W., Comanche Co., Oklahoma. This is the locality called the "Fort Sill Locality" by Gregory, Peabody and Price (1956, p. 3). These fissure deposits are of early Permian age, possibly (*loc. cit.*) of the same horizon as the Arroyo formation, lower Clear Fork group of Texas.

DESCRIPTION

Nothing remains of the left side of the skull. Of the right side only elements of the dermal skull roof and the teeth are preserved. The roof is fairly complete dorsally, but only the anterior two-thirds or so of the lateral portion remain, so that the region of the lateral temporal fenestra is poorly known. The longitudinal dorsal series of elements is complete with the exception of the postparietal. Only the maxilla is present of the marginal elements. All the elements of the circumorbital series are represented, but the postorbital and the jugal lack their posterior processes. There is no trace of any of the elements of the temporal series and the cheek. Except for the absence of a few teeth apparently lost post-mortem and the

[1] Published with the permission of the Secretary of the Smithsonian Institution.

loss of the distal tips of several others, the maxillary dentition is complete.

Several bones that cannot be identified lie in the matrix under cover of the dermal roof; some of these may be seen through the orbit. A metapodial lies in the same place, but, considering the general jumble of bones in the Fort Sill fissures, it would be unsafe to assume that they belong to the same species as does the skull.

Although there has been little displacement of the elements from their natural relationships with their immediate neighbors, and although the dorsal and lateral portions of the dermal roof retain, individually, what seem to have been their natural contours, the skull has been crushed in such a way that the dorsal portion meets the general lateral surface at an angle of about 75° (see Text-fig. 1C). Some of the natural curvature of the intermediate region remains, so that the dorsal portion of the postorbital meets the dorsal surface of the roof at an angle of about 120° while farther ventrally the postorbital lies in a plane almost perpendicular to this same surface. The crushing has opened the sutures between the parietal and the posterodorsal circumorbital elements, the suture with the prefrontal slightly, that with the postorbital widely.

The distance from the anteriormost limit of the nasal to the posterior end of the medial border of the parietal, measured along the midline, is 37.0 mm. Comparing this figure with the corresponding measurement in *Eothyris parkeyi* (Romer and Price, 1940, fig. 53; Watson, 1954, fig. 10), which pelycosaur *Colobomycter pholeter* most closely resembles, the total length of the skull, from tip of snout to hindmost point of quadrate, may be estimated at about 50 mm. The orbit is 13.5 mm. long and 11.5 mm. high. The interorbital distance was 12.0 mm. The depth of the skull is about 15 mm. through the center of the orbit and about 9 mm. at the posterior border of the naris. The distance from the orbit to the naris is 9.0 mm.

Most of the details of the structure of the skull can be easily made out from the figure, and it will be necessary only to add comments:

The nasal is narrow posteriorly but expands anteriorly and ventrally where it passes down in front of the prefrontal to its narrow contact with the lacrimal and broad contact with the maxilla. Posteriorly, it meets the frontal about midway in the length of the prefrontal. It gives the snout its dorsal convexity.

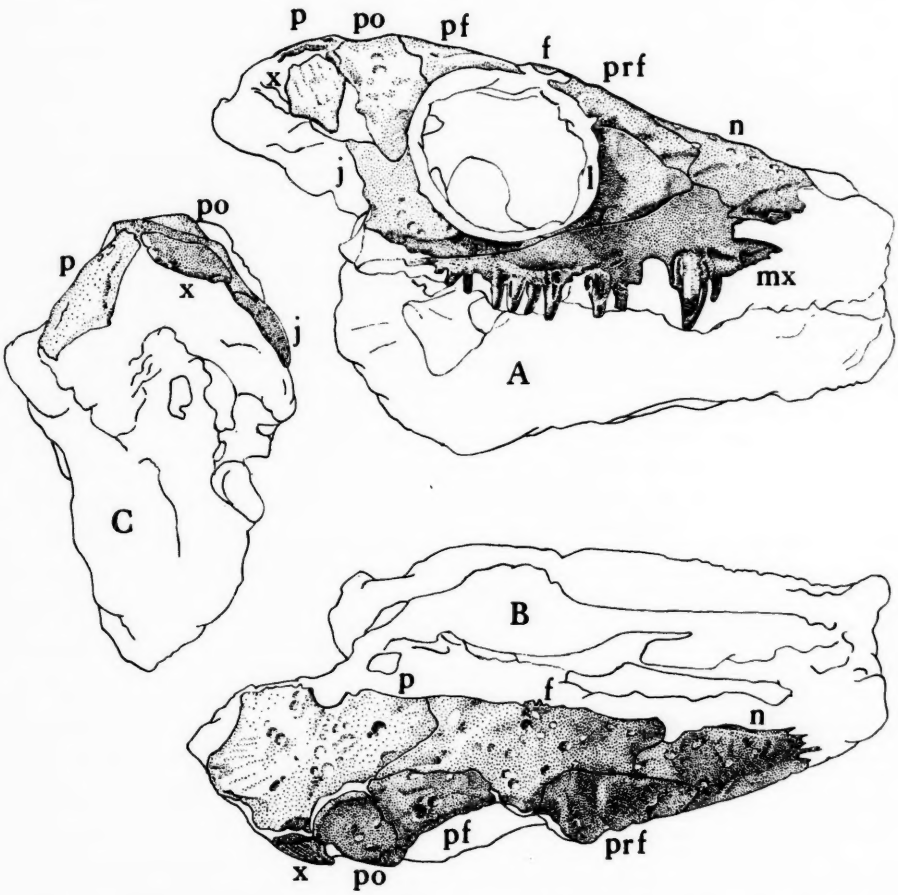
The frontal has broad contacts with the nasal, prefrontal and postfrontal. It has a lateral process that enters the orbit, restricted somewhat at its entrance by narrow processes from the prefrontal and postfrontal. There is a broad, posteriorly concave contact with the parietal. A narrow process passes posteriorly and laterally between parietal and postfrontal to come close to, but not touch, the postorbital.

A large, semilunar notch midway in the length of the medial border of the parietal indicates a sizable parietal foramen. Laterally, the parietal is in contact with the postorbital. Crushing in this region has caused the postorbital to override the lateral edge of the parietal, and it is probable that the latter element actually extended farther laterally, in a "parietal lappet" (Watson, 1954), than can be made out from the specimen; a thin band of matrix left under the disarticulated dorsal edge of the postorbital to protect it makes the parietal appear narrower than it is. The posteromedial border of the parietal is concave and presumably received the postparietal and tabular. There is a broad, rabbeted posterolateral edge, over which must have lain the anterior edge of a rather *large* supratemporal, unusual among pelycosaurs.

Except for the shortness of the contact between postfrontal and parietal, there is nothing unusual about the relationships of the pre- and postfrontals.

The lacrimal is cut off from the narial margin by the meeting of the nasal and a dorsal process of the maxilla. The contact with the nasal is a short one; most of the lacrimal's dorsal suture is with the prefrontal. Ventrally, the lacrimal sends a long, thin process under the orbit to meet a similar process from the jugal.

Except for the rather unusual curvature of its contact with the postorbital, the fragment of jugal preserved is of a normal shape. The portion of the jugal that overlay the posteriormost part of the maxilla is missing, but the smooth surface of the matrix in the region indicates its former presence there.



TEXT-FIG. *1*—Type specimen of *Colobomycter pholeter* n. gen. n. sp., C.N.H.M. U.R. 272. A, lateral; B, dorsal; C, posterior views. All ×2. Unshaded areas represent matrix. F, frontal; J, jugal; L, lacrimal; Mx, maxilla; N, nasal; P, parietal; Pf, postfrontal; Po, postorbital; Prf, prefrontal; X, indeterminate element.

Unfortunately, almost nothing is known of the posterior process that presumably underlay the lateral temporal opening. It is difficult to decide whether or not any portion of the posterior border of the fragment of jugal represents a fenestral edge. Most of this border shows evidence of breakage, but the two millimeters immediately dorsal to a posteriorly directed nub at the posteroventral corner of the fragment seem to be smoothly finished. If this small portion of the border *is* part of a fenestral edge, the nub may represent part of the posterior process of the jugal. In this case, the anteroventral angle of the temporal opening would have been acute and fairly sharp, but this is the condition in some other pelycosaurs too, e.g., *Varanops brevirostris* (see Romer and Price, 1940, pl. 5). The evidence is inconclusive.

The postorbital meets the jugal in a suture that at first passes anteriorly and ventrally and then, shortly before reaching the orbit, swings dorsally. The curvature of this suture is unusual but is not unmatched; the corresponding suture looks much the same in *Sphenacodon ferox* (see Romer and Price, 1940, fig. 4E). Usually, the suture

continues in an anteroventral direction all the way to the orbit. The posterior part of the postorbital is missing; not even enough of this portion remains to complete the contact with the jugal, and, consequently, we know nothing of the process that presumably overlay the lateral temporal opening.

In the posterolateral angle formed by the parietal and the portion of postorbital preserved lies a completely disarticulated fragment of bone. From its flatness and the pitting on its surface, it is quite obvious that this is a piece of a roofing element. The edge of the rounded front upper corner of the fragment is beveled on its external surface. This beveled edge is smooth in its front part, possibly indicating clean breakage from the main body of the element, and bears small striae perpendicular to the border in its upper part, probably indicating an area overlain by a neighboring element. This neighboring element may have been the parietal, and the fragment may be a part of the posterior process of the postorbital. I am inclined to consider the fragment as indeterminate.

The posteriormost portion of the maxilla is missing, but the rate of narrowing of this element as indicated by the infraorbital portion preserved indicates that it extended no farther posteriorly than the posterior border of the fragment of jugal. The maxilla has its greatest depth immediately anterior to the lacrimal, where it carries the large canine tooth. Anterior to this, the dorsal border of the maxilla slopes downward to the posterodorsal corner of the naris. Immediately anterior to the base of the large canine, the surface of the maxilla is impressed by a deep groove, which has a narrow posterodorsal apex and a broad mouth that is confluent with the dentigerous rim at the base of the first maxillary tooth. The function of this groove is not clear; possibly, a foramen opening into the apex carried nerves and/or blood vessels from the interior of the snout. Below the naris the ventral border of the maxilla slopes upward as a ragged edge, undoubtedly for the reception of an underlying process of the premaxilla.

All of the posterior border of the naris is formed by the maxilla. Except, of course, for the role of the premaxilla, the dorsal border is formed by the nasal. At the ventral border of the naris, the maxilla is shaped into a broad rim, whose surface slopes downward and outward, so that the narial opening appears much larger when viewed in a line at about 45° to the surface of the maxilla; in a strictly lateral view (as in the figure) the full size of the naris cannot be appreciated.

The external surfaces of the longitudinal dorsal elements and of all the circumorbital elements except the lacrimal are ornamented with scattered pits. The external surface of the maxilla is not well enough preserved to permit any statement as to whether or not it was pitted. The posterior part of the external surface of the lacrimal is not well preserved, but the anterior part is, and it is smooth.

Eleven maxillary teeth are present in C.N.H.M. U.R. 272. Gaps indicate the former presence of several more. The largest tooth is the second in the maxillary series and lies directly below the dorsalmost extension of the maxilla. The lateral wall of its socket is broken away, and the whole length of the tooth may be seen. The shape of this tooth is basically conical, but definite anterior and posterior edges are present; the same may be said in general of all the maxillary teeth. This largest tooth is slightly recurved, and so is the tooth anterior to it, but no recurvature can be detected in any of the other teeth. The total length of this tooth, from base to tip, is about 5.0 mm., and it projects about 3.5 mm. beyond the rim of the maxilla. Although the lateral wall of the socket is missing, the swollen nature of the bone directly anterior to this tooth—and behind the mouth of the groove in the maxilla—indicates the former presence of a bulge in the external surface of the bone in this region.

The anteriormost maxillary tooth projects about 1.6 mm. beyond the rim of the maxilla, but it is set in rather deeply from the lateral surface of the skull, and it is held in a socket that has a diameter about twice as great as the diameter of the base of the tooth. It is quite apparent that this is an early stage of a replacement tooth, a tooth that would have grown to be proportionately much larger had the specimen remained alive longer than it did. This anteriormost

maxillary tooth—in its mature length—and the tooth immediately posterior to it probably formed a pair of "canines," the second larger than the first as evidenced by the fact that the second lies under the dorsalmost extension of the maxilla (this matter is discussed again below).

Directly posterior to the largest tooth there is a gap where a small portion of the maxilla is missing. Judging from the length of the gap, from the size and spacing of the teeth posterior to it, and from the fact that there seems to be a steady anteriorward decrease in size from midway in the row of postcanine teeth, the gap probably represents two missing teeth, but possibly only one. The largest tooth behind this gap lies almost exactly midway in the postcanine series and had, allowing for its missing tip, an extramaxillary length of about 2.7 mm. Anterior and posterior to this tooth, the teeth gradually decline in length; the posteriormost tooth is so small that it is extremely doubtful that another tooth occurred behind it. Two gaps in the postcanine series other than the one already described seem to represent one missing tooth apiece. If the above analysis is correct, there were, in the maxilla, two canine and thirteen postcanine teeth.

COMPARISONS WITH OTHER PELYCOSAURS

Very little, almost nothing, is known of the region of the lateral temporal fenestra in *Colobomycter*, and this may lead to the suspicion that what we are dealing with is actually a captorhinomorph of some kind—perhaps a romeriid. Romer and Price (1940, p. 180) have pointed out that "Between the progressive features of advanced cotylosaurs and the primitive features retained in ophiacodont pelycosaurs, we have left of diagnostic value for separation between the two groups only the debatable ground of neural arch evolution and the actual presence or absence of the temporal opening. The opening is thus the only valid diagnostic feature of a pelycosaur." In the absence of positive evidence for this diagnostic feature in the specimen C.N.H.M. U.R. 272, what grounds justify its identification as a pelycosaur?

There is no possibility of any connection with microsaurs. The pattern of parting of the sutures of the dermal skull roof under crushing pressure indicates the presence of a persistent line of weakness in the position of the ancestral otic notch. This line of weakness is commonly found in primitive pelycosaurs and captorhinomorphs (see Watson, 1954), whereas "In microsaurs the otic notch has been . . . so thoroughly obliterated that dermal cheek and table elements are welded into a single unit" (Romer, 1950, p. 645). And *Colobomycter* is obviously not a diadectomorph. Considering horizon and geography, the only group outside of the Pelycosauria that *Colobomycter* might be thought to belong to would be the Captorhinomorpha, and the only similarity here would be with the romeriids; *Limnoscelis* is much too primitive, the captorhinids have striking specializations, and the only similarity to *Araeoscelis* is in size. It must be admitted that there are certain resemblances to the romeriids (see Watson, 1954, figs. 7, 8, 9), but, in the ways in which it resembles the romeriids, *Colobomycter* also resembles the pelycosaurs—the two groups are generally considered to be closely related—and it is only among pelycosaurs that we find matches for the distinctive features of *Colobomycter:* the short face, the exclusion of the lacrimal from the narial margin, and the placement of the largest maxillary teeth very far forward. Besides this, *Colobomycter* seems to be in some ways a structural intermediate between *Eothyris* and the caseids. With reference to this last point, however, the possibility of a polyphyletic origin of the pelycosaurs must be kept in mind: Watson (1957, fig. 23) has the caseid line drawn as a distinctly separate branch of pelycosaurs in his phylogenetic chart, and Romer and Price (1940, p. 181) consider a polyphyletic origin of pelycosaurs quite possible. But although it is possible that *Colobomycter* may represent a line derived independently of other pelycosaurs from the romeriids and going on, perhaps, to give rise to the caseids, with *Eothyris* and company possibly off on a side branch, these possibilities seem unnecessarily complicated in view of the limited information on hand. Considering its general structure, its advanced features, and its resemblances to eothyridids and caseids (to be enumerated below), it seems quite safe to believe that *Colobomycter* was a pelycosaur.

Interestingly, and significantly, *Colobomycter* shows similarity to members of families of *two* of the suborders of Pelycosauria. There is little real resemblance to sphenacodonts; most of the resemblances that do exist are in characters obviously inherited in common from remote ancestors, e.g., contact of the lacrimal and jugal, and these are found in members of all three suborders. Varanopsids and *Colobomycter* are alike only in the common retention of some primitive features. Advanced sphenacodontids have the lacrimal excluded from the narial margin, but this is undoubtedly the result of a parallel trend within the sphenacodontids to dorsalward growth of the maxilla associated with enlargement of the canine teeth; the lacrimal reaches the naris in primitive sphenacodontids. Within the Ophiacodontia, the ophiacodontids themselves are quite different from *Colobomycter* with their "skull large, relatively narrow and moderately to greatly elongated in the facial region; marginal teeth numerous, including 40–55 in upper jaw; canines little developed, and a number of precanine maxillary teeth present." (Romer, 1956, p. 675), but when one examines the eothyridids, definite evidences of affinity are seen. *Colobomycter* differs considerably from the highly specialized Edaphosauridae, but it bears marks of close affinity with the caseids and may, therefore, be suspected of relationship also with the nitosaurid edaphosaurs. Accordingly, *Colobomycter* may be profitably compared with eothyridids, nitosaurids, and caseids.

Romer (1956, p. 676) feels that the eothyridids are possibly a composite group, and that they might, "if better known, . . . represent several lines of evolution among primitive pelycosaurs." Romer (*loc. cit.*) defines the family as: "Ophiacodontoids paralleling the sphenacodonts in the development of enlarged canines and showing a tendency toward elongation of the vertebral column." The skull in the European *Stereorachis* and that in *Stereophallodon* from the Pueblo formation of Texas are known only from fragments that are of little use to us here, but *Eothyris* is known from a fairly complete skull from the Belle Plains formation of Texas, and *Baldwinonus dunkardensis*, from the Dunkard series of Ohio, is known from an interesting and important maxilla.

The likeness of *Colobomycter* to *Eothyris* is readily seen (for *Eothyris*, see Romer, 1937, pl. V; Romer and Price, 1940, figs. 3F, 53; Watson, 1954, figs. 10,11,12). The most immediately apparent resemblance, approximation in size, is perhaps the least significant. The skull in *Eothyris parkeyi* is 62 mm. long, that in *Colobomycter pholeter* about 50 mm. These skulls are among the very smallest to be found among pelycosaurs, and that of *C. pholeter* is perhaps the smallest, with the skull of *Glaucosaurus megalops*, at 52 mm. in length, the next larger. More significant resemblances are:

(1) Shortness of face. In both, the interorbital distance is slightly less than the length of the orbit and is approximately one and one-third times as great as the distance from the orbit to the naris. This shortness is not the result of any great enlargement of the orbit; in neither form does the orbit bulge to any appreciable extent above the general level of the dorsal surface of the skull, as it does in other small pelycosaurs as *Mycterosaurus* and *Glaucosaurus*. This shortness of face in both *Eothyris* and *Colobomycter* seems extremely significant when one considers that up until this time one could say that "the face [in *Eothyris*] is shorter by far than in any other pelycosaur except edaphosaurs" (Romer and Price, 1940, p. 249).

(2) A postorbital bar of considerable anteroposterior thickness. In *Eothyris*, the thickness of the postorbital bar is equal to almost one-quarter the length of the orbit. The available evidence indicates that the same ratio holds for *Colobomycter*. This character is not limited to *Eothyris* and *Colobomycter*—the postorbital bar is nearly as thick in *Varanops*—but it does serve to distinguish these two from other small American pelycosaurs; the bar is much thinner in *Glaucosaurus*, *Mycterosaurus* and *Casea*.

(3) If its dimensions may be estimated from the length of the rabbeted posterolateral edge of the parietal in C.N.H.M. U.R. 272, the large size of the supratemporal in *Colobomycter* is matched among pelycosaurs only by that in *Eothyris*, in which, according to Romer and Price (1940, p. 250), this element is proportionately larger than in any other pelycosaur.

(4) Both *Colobomycter* and *Eothyris* have a large parietal foramen.

(5) The naris is large in both. As restored by Romer and Price (1940, fig. 3F) the naris in *Eothyris* is of normal proportions, but it is drawn much larger in a later restoration by Watson (1954, fig. 12), who notes (*ibid.*, p. 356) that "the outer surface of the internarial processes [of the premaxillae] slopes upward and forward so as to show that the nostrils were enlarged, as in *Casea*."

(6) Unfortunately, nothing is known of the premaxillary dentition in *Colobomycter*, but it can be readily seen that the maxillary dentition is very much like that in *Eothyris*. Romer and Price (1940, p. 251) state that in *Eothyris* "The premaxilla carried three teeth . . . precanine maxillary teeth have disappeared completely . . . ." In Romer's illustration of the actual specimen of *E. parkeyi* (1937, pl. V), and in the reconstruction by Romer and Price (1940, fig. 3F), a small tooth lies ahead of the first canine in a position posterior to the external line of the suture between premaxilla and maxilla; Watson's reconstruction (1954, fig. 12) shows the same condition, and in both these reconstructions, the premaxilla carries only two teeth anterior to this external line. Apparently, as is the situation in *Dimetrodon limbatus* (Romer and Price, 1940, pl. 13), the last premaxillary tooth is attached to an extension of the premaxilla that passes posteriorly under external cover of the maxilla (although, due to a narrow exposure of this process ventral to the maxillary cover, the tooth in *D. limbatus* may be seen even in lateral view to be carried by the premaxilla). The single seemingly precanine tooth in C.N.H.M. U.R. 272 is definitely on the maxilla, but it is an odd tooth in that it is set in such a large socket, a socket about twice as wide in diameter as the base of the tooth. This tooth cannot be mature; it was evidently arrested at an early stage in the replacement of a larger canine tooth. This first canine—even when mature—was probably somewhat smaller than the second, as in *Eothyris*, and, again as in *Eothyris*, the larger canine was located almost directly below the dorsalmost expansion of the maxilla, with the smaller canine below the region where the dorsal border of that bone slopes downward to the narial margin. That the first canine would have been smaller than the second is supported not only by the location of the second in the deepest part of the maxilla, but also by the indication of an outward swelling of the maxilla around the base of the second canine. A difference from *Eothyris* would be that a small anterior portion of the mature first canine in *Colobomycter* would lie directly below the naris whereas in the former the first canine lies entirely behind the naris—although the anterior border of this tooth in *Eothyris* lies very near the plane of the posterior border of the naris. There were apparently twelve postcanine teeth in *Eothyris*, according to the restorations by Watson and by Romer and Price. Assuming that the first gap in the maxillary tooth row in C.N.H.M. U.R. 272 represents two missing teeth, and that the posterior two gaps represent one apiece, *Colobomycter* must have had about thirteen postcanine teeth; even allowing for a possible error of one or two in estimating the number of missing teeth, this is a remarkably close resemblance. As in *Eothyris*, there seems to have been a second region of (less pronounced) elongation of the teeth about halfway along the postcanine row.

The outstanding differences between *Colobomycter* and *Eothyris* are:

(1) The frontal does not enter the orbit in *Eothyris*. *Eothyris* is unique in this way among pelycosaurs (Romer and Price, 1940, p. 249). This is a primitive condition.

(2) The lacrimal is excluded from the narial margin in *Colobomycter*, and in this too, *Colobomycter* is advanced beyond *Eothyris*.

(3) Although the contact is a narrow one, the lacrimal in *Colobomycter* meets the jugal, and this is more primitive than the condition in *Eothyris*.

(4) The dermal skull roof in *Colobomycter* is pitted. This condition is duplicated among pelycosaurs only by the caseids. According to Romer and Price (1940, p. 415), "The pitted skull roof [in caseids], unmatched in other pelycosaurs, suggests the presence of a tough, leathery skin. . . ." If Watson is correct in his suspicion when he says (1954, p. 356) "Indeed it is not inconceivable that *Eothyris* may be an ancestor of the Caseids . . .," the presence of the pits in *Colobomyc-*

ter may be regarded as an advance over *Eothyris* in the progression toward caseids.

Thus, two of the differences between *Eothyris* and *Colobomycter* are due to persistence of primitive characters in *Eothyris*, one of the differences is due to the persistence of a primitive character in *Colobomycter*, and one difference probably represents an advancement in *Colobomycter* in a phylogenetic line to which *Eothyris* is thought to belong. The ways in which *Colobomycter* resembles *Eothyris*, taken individually, are highly suggestive of relationship; taken together, they make it certain that the two are very closely related.

Of the skull of *Baldwinonus trux*, from the New Mexico lower Permian, only a maxilla and a portion of the quadrate are known. The canines are enlarged, but there are about five precanines and about two dozen postcanines (Romer and Price, 1940, p. 256, fig. 54). Besides this, *B. trux* is well over six times as large as *Colobomycter pholeter*. There are no similarities.

Baldwinonus dunkardensis, from the Washington group of the Dunkard series of Ohio, seems to have been quite different from *B. trux*, and it was with some doubt that Romer (1952, p. 96) referred it to *Baldwinonus*. Unfortunately, it is known only from a maxilla, but, although this bone indicates a pelycosaur of over three times the size of *Colobomycter pholeter*, there are some similarities. *B. dunkardensis* had two canines followed by a row of smaller teeth (the number of which is unknown). Another point of resemblance is the presence of a far dorsalward extension of the maxilla above the second canine in *B. dunkardensis;* possibly this extension kept the lacrimal from the narial margin. A major difference, assuming that the foregoing analysis of the dentition in *Colobomycter* is correct, would be in the presence of a moderately sized precanine tooth on the maxilla in *B. dunkardensis*. Further comparison is not worthwhile. *B. dunkardensis* is probably an eothyridid, as evidenced by the two canines, the first of which lies entirely anterior to the dorsal process of the maxilla, but it is doubtful that it is congeneric with *B. trux*, and the latter may not even belong in the same family.

Tetraceratops, from the Arroyo formation of Texas, is provisionally assigned by Romer (1956, p. 676) to the Eothyrididae, but its strange specializations would make any relationship to *Colobomycter* a remote one.

The Nitosauridae are defined by Romer (1956, p. 680) as "Small, primitive edaphosaurs, with few specializations. Face moderately elongate, jaw articulating on a level with tooth row; jaw of primitive type. The teeth sharp, subisodont, with some development of incisor and canine regions; palatal dentition primitive . . . [plus a postcranial diagnosis]."

Romer (*ibid.*, p. 681) tentatively assigns *Puercosaurus* and *Glaucosaurus* to the Nitosauridae. *Puercosaurus*, a very small form from the New Mexico lower Permian, is at present poorly known, but, on the basis of the account given by Williston (1916, p. 190–191, fig. 37), we may at least be sure that it is not congeneric with *Colobomycter*. According to Williston's description of *P. obtusidens*, "The eighth of the maxillary series [of fourteen or fifteen teeth] is much larger than the others, either in front or behind, though not much longer." *Glaucosaurus* (see Romer and Price, 1940, p. 421, pl. 20), from the Clyde formation of Texas, is likewise poorly known. It is interesting here in that the skull in the only known species is only 52 mm. long—about the same size as that in *Colobomycter pholeter*—and in that it has an extremely short face; but it has bulging orbits, the marginal teeth are isodont, and the skull roof is not pitted. Romer and Price (*loc. cit.*) consider *Glaucosaurus* to be related to the caseids, and it is possible, therefore, that it may be related to *Colobomycter*, but the lack of visible sutures in the skull would make further comparison of little value. *Nitosaurus* (see Romer and Price, 1940, p. 406–408, fig. 70), from the Abo formation of New Mexico, is known from enough of its postcranial structure to indicate relationship with the caseids, but of its skull only fragments of the jaws are available. These show that the teeth in the anterior part of the maxilla were shorter than those farther back; further comparison of skull structure is not possible.

Mycterosaurus (see Romer and Price, 1940, pl. 21), from the Clyde formation, is the best known nitosaurid. *Eumatthevia* Broom is a synonym (*loc. cit.*). The skull in

Mycterosaurus, 89 mm. long in the only known species, bears few resemblances to that in *Colobomycter*, but there is similarity in a rare character: exclusion of the lacrimal from the narial margin. Until this time, this feature has been known among pelycosaurs only in *Mycterosaurus* and in advanced sphenacodonts (Romer and Price, 1940, p. 409). *Mycterosaurus* differs from *Colobomycter* in the following ways: The face is elongate; the orbit bulges well above the general level of the dorsal surface of the skull roof; the postorbital bar is narrow; the skull roof is not pitted; the lacrimal is, or is almost, kept from touching the nasal by a narrow contact of the maxilla with the prefrontal; the lacrimal fails to meet the jugal; and the longest teeth in the maxilla lie about one-third way back in the maxillary series. The reasons for believing that *Colobomycter* is in some way related to *Mycterosaurus* are: The nitosaurids can be seen from their postcranial anatomy to be probably related to the caseids; *Glaucosaurus*, also probably related to caseids, may be considered a tie between *Colobomycter* and *Mycterosaurus* in the matter of length of face. The exclusion of the lacrimal from the naris may be phylogenetically significant, but more likely this is a matter of parallel development in association with elongation of teeth. The postcranial evidence for nitosaurid-caseid relationship is the most important factor.

Romer (1956, p. 681) defines the family Caseidae: "Skull rugose, relatively small, low, short, but broad; a large parietal foramen, an enormous narial opening, a pronounced rostrum. Jaw articulation well below level of tooth row. Supraoccipital little expanded laterally; paroccipital plates greatly expanded. No retroarticular process on jaw. Marginal teeth isodont, blunt; palatal teeth strongly developed but not concentrated in toothplates; little or no tooth development on coronoid . . . [plus a postcranial diagnosis]." The American genera of Caseidae are *Angelosaurus*, *Casea*, *Caseoides* and *Cotylorhynchus*. The skull of *Angelosaurus* is known only from fragments, and the skull of *Caseoides* is not known at all; besides this, these two genera occur only in the lower middle Permian of Texas, in the San Angelo formation; they need not be considered. *Ennatosaurus*, from Zone I or younger of the Russian Permian, differs from *Casea* and *Cotylorhynchus* principally in dental pattern (Olson, 1957).

Casea broilii was long thought to occur in the Arroyo formation of Texas, but Olson has recently (1954, p. 193) pointed out that the horizon is actually lower Vale. The upper Vale species, *C. nicholsi*, is known in its skull only from fragments of the posterior dermal roof and the palate, and nothing is known of the skull in the Choza species, *C. halselli* (Olson, 1954). The skull in *Cotylorhynchus*, from the Hennessey formation of Oklahoma, is well known. The skull in *Cotylorhynchus romeri* is considerably longer than that in *Casea broilii*, 178 mm. as compared to 79 mm. (Romer and Price, 1940, fig. 7), but the two are very much alike, and the skull in *Colobomycter* may be compared with, simply, the "caseid skull." Outstanding resemblances are:

(1) Rugosity. Among pelycosaurs now known, the skull roof is pitted only in *Colobomycter* and the caseids.

(2) Shortness of face. In this, the caseids have gone to the extreme; only a thin bar remains between orbit and naris. The lacrimal enters the naris, but Romer and Price (1940, p. 412) offer a possible reason why this may be secondary: "Extension forward of the lacrimal to the naris in primitive pelycosaurs is surely associated with stimulation toward ossification caused in this area in the embryo by the presence of the lacrimal duct. If we assume provisionally that the peculiar type of narial development present in caseids had already been initiated in *Mycterosaurus*, it is probable that the duct would have been shortened or have lain at a deeper level, and hence the former stimulus caused anteriorly by its presence would have been removed. In any event, it will be noted that if the narial opening were enlarged in *Mycterosaurus* to the extent seen in caseids, the lacrimal, although abbreviated, would reenter the posterior margin of the opening."

(3) A large naris. In caseids the naris is a huge opening with rims above and below that diverge as they pass outward, giving the naris the aspect of a crater. The naris in *Colobomycter*, although not completely known, must have been large, and its ventral rim resembles that in the caseid skull.

(4) Large supratemporal. The sutures in

this region in *Cotylorhynchus* (Romer and Price, 1940, pl. 19) are not clearly known, but the supratemporal in *Casea* (*ibid.*, pl. 20) is very wide. The element itself is missing in C.N.H.M. U.R. 272, but, from the evidence available, there does seem to be a very real and significant resemblance here.

(5) The parietal foramen is large in *Colobomycter* and the caseids.

(6) *Cotylorhynchus* has an "infraorbital foramen" on the maxilla immediately behind the posteroventral corner of the naris (Romer and Price, 1940, pl. 18). Possibly the groove in this region in *Colobomycter* is an homologous structure.

The caseids are, obviously, a highly specialized family, and there are naturally considerable differences from *Colobomycter*. Chief among these are:

(1) As noted above, entrance (re-entrance?) of the lacrimal into the narial margin, possibly as a consequence of the extreme shortness of face.

(2) The teeth in caseids increase gradually in length from the posterior end of the maxillary series to: in *Casea*, the anterior end; in *Cotylorhynchus*, a region about quarter-way back, anterior to which they decrease gradually in length.

(3) The postorbital bar is narrow in caseids.

(4) The caseids have a remarkable, pointed rostrum. The rostrum in *Colobomycter* is unknown, but Watson (1954, fig. 12) restores that of *Eothyris* as similar to that in caseids. Perhaps *Colobomycter* was like the caseids in rostral structure.

PHYLOGENETIC POSITION OF COLOBOMYCTER

Colobomycter is clearly related to *Eothyris*. Considering the features in which both *Colobomycter* and *Eothyris* resemble the caseids, there seem to be definite evidences of fairly close relationship with this family, and this is in accord with the suspicions already expressed by Watson (1954, 1957). The presence of a rugose sculpture on the skull roof in *Colobomycter* would seem to confirm these suspicions. *Eothyris* is known only from the Belle Plains formation, *Colobomycter* is known only from deposits possibly equivalent in age to the Arroyo formation, and *Casea* first appears in the lower Vale. These formations follow one another in the stratigraphic column, and, possibly, the series *Eothyris-Colobomycter-Casea* represents a genuine phylogenetic sequence. That the lacrimal does not touch the naris in *Colobomycter* would not disturb this sequence if Romer's theory of primary reduction of this element followed by its re-entrance into the narial margin in the caseid line is correct, but this theory needs the proof of intermediate forms. That the lacrimal does not meet the jugal in *Eothyris* would seem to be an advancement in at least one respect beyond conditions in *Colobomycter*, and may indicate advancement in other features as well. Probably, the origin of the caseids is to be sought in a time prior to the deposition of the Belle Plains formation. This view would seem to receive support from the presence of an as yet undescribed, apparently primitive caseid in the Abo formation of New Mexico (see Olson, 1954, p. 193); the Abo formation is generally considered to be equivalent in age to the lower and middle parts of the Wichita group of Texas. *Eothyris* and *Colobomycter* probably represent side branches from the phylogenetic line leading to the caseids, with the branch leading to *Colobomycter* leaving the main line later than the branch leading to *Eothyris*. The nitosaurids probably left the main line at a much earlier time.

Colobomycter could possibly be classified as a caseid. But the extremely short distance between orbit and naris—with entrance or re-entrance of the lacrimal into the narial margin—and the highly specialized rostrum in the caseids make theirs a rather exclusive group, and, especially in view of the fact that the rostrum in *Colobomycter* is unknown, I feel that this new pelycosaur is better assigned to a more primitive family, but to a family that has definite connections with the Caseidae. The nitosaurids are such a family, their relationship to the caseids established by studies on their postcranial anatomy, but the skull in *Colobomycter* resembles much more that in *Eothyris* than it does that in any nitosaurid—and the suspicion of Watson that *Eothyris* is implicated in the origin of the caseids is supported by this similarity. Perhaps in default of better knowledge of the families concerned—and of *Colobomycter*—but perhaps also reason-

ably with respect to the knowledge on hand, I feel that *Colobomycter* is best referred to the Eothyrididae. The important facts are that knowledge of *Colobomycter* helps to bind all three families together in the phylogenetic scheme, and that *Colobomycter* provides a good structural if not an actual ancestor for the family Caseidae.

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VARIATION IN *GONIORHYNCHIA BOUETI* FROM NORMANDY AND DORSET

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ABSTRACT—The external characters of individuals of *Rhynchonella boueti* Davidson from Normandy and Dorset have been analyzed by means of various biometrical methods. From the analysis of the frequency distributions of the bio-characters, collections have been found to be homogeneous, although subjected to various secondary sorting effects. By a comparison of shape parameters, however, the collections are grouped into two sub-species (one from Normandy and one from Dorset) of a single species. The possible ecological basis of the variation is discussed with reference to living brachiopods.

INTRODUCTION

Rhynchonella boueti Davidson is a characteristic fossil of the Boueti bed, a thin calcareous clay in the Great Oolite Series. In the present work an attempt is made to study the geographical variation of *R. boueti* by means of a biometrical comparison between the collections from Dorset and Normandy.

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HISTORY

Rhynchonella boueti was first described by Davidson (1852, p. 254, pl. XIII, figs. 4,5) from the Great Oolite of Ranville near Caen. Two specimens were figured, a dorsal view of a shell and an internal view of an open pedicle valve. The figured specimens are in the British Museum, Natural History (Registered numbers B.5512). The collection consists of eleven specimens, including the figured open pedicle valve. The other specimen figured by Davidson cannot be identified precisely.

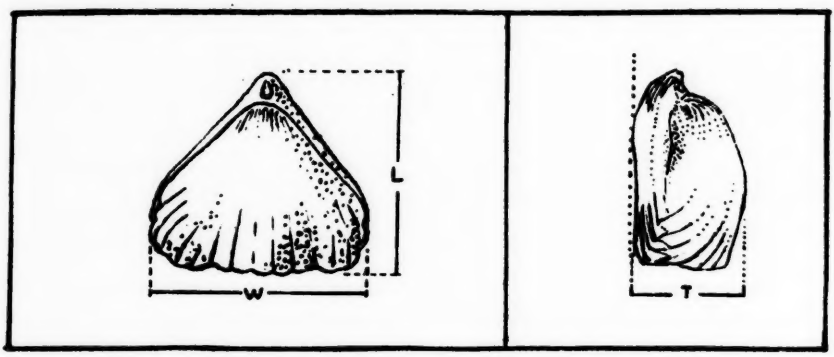
R. boueti was stated by Davidson to differ from *R. obsolata* Sowerby, with which it occurs in great abundance, by its more elevated and pinched-in mesial fold and by its trilobed character. The dimensions of *R. boueti* given by Davidson are: Length 1 inch (25 mm.), width 1.2 inches (30 mm.), thickness 0.7 inch (17.5 mm.).

The description of *R. boueti* was later included by Davidson in his monograph and the specimen was recorded for the first time from Britain (1878, p. 197, pl. XXVI, figs. 15,16). This figured specimen is also in the British Museum, Natural History (Registered numbers B.27331), and comes from Langton Herring in Dorset. Other localities where the species had been found in Britain were also noted. Davidson's own collection of *R. boueti* from Burton Bradstock (another locality in Dorset) consists of three specimens (Registered number B.12030) in the British Museum, Natural History.

Later, Buckman (1917, p. 52, pl. XVIII, figs. 22,23) subdivided the English specimens referred by Davidson to *R. boueti* into two distinct species, under a new generic name *Goniorhynchia*.[1] In doing so he remarked (loc. cit.):

> "*R. boueti* Davidson covers several different species which it is necessary to separate: the name was given in the first case to a rather coarse-ribbed form.

[1] Pending a revision of the Jurassic Rhynchonellids Buckman's genus is here retained for the species studied.



TEXT-FIG. *1*—Unit characters of *Goniorhynchia boueti*.

The Tripartite and Trigonal character of the *R. boueti* forms is often very distinct. Internally, they show considerable posterior calcification and externally, signs of old age."

Buckman's two species were called *G. goniaea* (pl. XVIII, figs. 22a,d) and *G. contracta* (pl. XVIII, figs. 23a,aa,c,d,dd), of which *G. goniaea* was taken as the type of *Goniorhynchia*. These two figured specimens are in the Geological Survey and Museum (Registered numbers 31936 and 31937 respectively).

In distinguishing the two species Buckman added in the appendix of his monograph (p. 229):

> "*G. goniaea*, Davidson's 1878 figure differs decidedly from his 1852 species in shape and ribbing. *G. goniaea* differs from Davidson's 1878 species in having a broader fold not so much elevated, and in being a rather smaller shell; otherwise the likeness is close.
>
> *G. contracta*, a narrower form than *G. goniaea*, with a more tumid dorsal valve, a narrower sulcus and more elevated fold-line."

According to Buckman the specimens collected by him from Eype Mouth and Burton Bradstock were distinct, those from the former being referred to *G. goniaea* and those from the latter to *G. contracta*. He pointed out that both localities were at the same horizon i.e. the Boueti bed, which he called "Forest Marble Rhynchonella Bed." It is noteworthy that Langton Herring, where "*G. boueti*" occurs in great abundance, was not mentioned by Buckman, nor did he mention the occurrence of *boueti*, s. str., in England.

In the following table the specific names given to "*G. boueti*" from different localities by Davidson and Buckman are summarized:

	Davidson 1852	Davidson 1878	Buckman 1917
Ranville	boueti	boueti	boueti
Langton Herring	—	boueti	—
Burton Bradstock	—	boueti	contracta
Eype Mouth	—	—	goniaea

Alkins (1923) and Aitken & McKerrow (1948) have made biometrical studies of *G. boueti* on the basis material collected from Langton Herring. Both studies showed that the Langton Herring population is homogeneous. Mercier (1937) studied the variation of *G. boueti* from six different places (including the original locality, Ranville) in Normandy, but failed to show any difference between his collections.

LOCALITIES OF COLLECTION

A total of 736 specimens was used for biometrical analysis. The localities are listed below. Arkell (1947) may be consulted for precise location and description of the outcrops of the Boueti bed in the British area, and Mercier (1932) for the French area.

(1) Ranville in Normandy, collected by Davidson, consists of 10 specimens, kept in the British Museum, Natural History (Reg. no. B5512).
(2) Langton Herring in Dorset, collected by the author, consists of 600 specimens.
(3) Burton Bradstock in Dorset, collected by J. F. Walker, consists of 29 specimens (26 have been used), kept in the British Museum, Natural History (Reg. no. B12030).
(4) Eype Mouth in Dorset, collected by the author, consists of 100 specimens.

MEASUREMENTS

Characters which are suitable for biometric analysis can be divided into two groups: (i) *unit characters* and (ii) *simple or numerical characters.*

Unit Characters

(a) Length — Maximum distance from anterior margin to the beak of the pedicle valve in the plane of symmetry of the shell. (text-fig. 1,L)

(b) Width — Maximum distance between the two lateral margins at right angles to the plane of symmetry. (text-fig. 1,W)

(c) Thickness — Maximum distance between the two valves at right angles to the two lines representing length and width respectively. (text-fig. 1,T)

Numerical Characters

(a) Number of costae on the brachial valve.
(b) Number of costae on the pedicle valve.
(c) Number of costae on the brachial fold.

All linear measurements were made with vernier calipers. Ribs were counted along the shell margin with the help of a dissecting needle.

FREQUENCY DISTRIBUTION OF LENGTH, WIDTH AND THICKNESS[2]

Relevant statistics are shown in Table 1 and frequency histograms in text-figs. 2–4. In both the Langton Herring and Eype Mouth collections the frequency distributions of length, width and thickness are unimodal, and from the estimates of the coefficient of variation it is apparent that of the three variables thickness shows the greatest variation. The Normandy and Burton Bradstock collections are also unimodal in distribution, but in these cases the samples are too small to show any bimodality there may have been.

Tests have been carried out to estimate whether any of the samples depart significantly from normality.

In the case of the Langton Herring sample, length and thickness show significant negative skewness ($P<0.01$), but the distribution of width is approximately symmetrical ($0.2>P>0.1$).

The Eype Mouth sample shows skewness only in respect of the length and width where it is just significant at the 1% level, although unlike Langton Herring this is a positive skewness.

Boucot (1953) has shown that size frequency distribution of animals, specially marine organism such as pelecypods and brachiopods resembles the shape of their mortality curve. Percival (1944) demonstrated that juvenile mortality among *Terebratulla inconspicua* is very high, overcrowding, starvation and obstruction to growth caused by various obstacles in the substratum, being the main reasons. Consequently most of the frequency distributions of *T. inconspicua* showed marked positive skewness. Hemmingsen (1934) showed that positively skewed size frequency distributions are common both in living and fossil populations.

In the present work the frequency distribution of the different bio-characters of Langton Herring (length and thickness) show negative skewness while the Eype Mouth collection shows positive skewness (except for thickness). If Percival's (1944) observations and those of Deevey (1947) on positively skewed distribution in oysters are taken as typical of the mortality distributions of marine animals, then the negative skewness and normal distribution of the Langton Herring and Eype Mouth samples respectively must be considered to be the effect of some secondary action—such as for example sorting by waves, or post depositional selective destruction by (for instance) percolating solutions.

The means of bio-characters are compared in Table 2. For both width and thickness there are significant differences at 1% level between Langton Herring and Eype Mouth. Moreover the means for all three characters of the Normandy collection are significantly larger even than that of Eype Mouth. Langton Herring and Burton Bradstock possess the smallest individuals and they are very similar in nature. The observed size differences may, however, be due to secondary action rather than being inherent in the communities concerned, hence

[2] The Author's M.Sc. thesis, deposited in the Library of the University of London, may be consulted for more detailed figures of frequency distributions, etc.

TABLE 1—ORIGINAL DATA

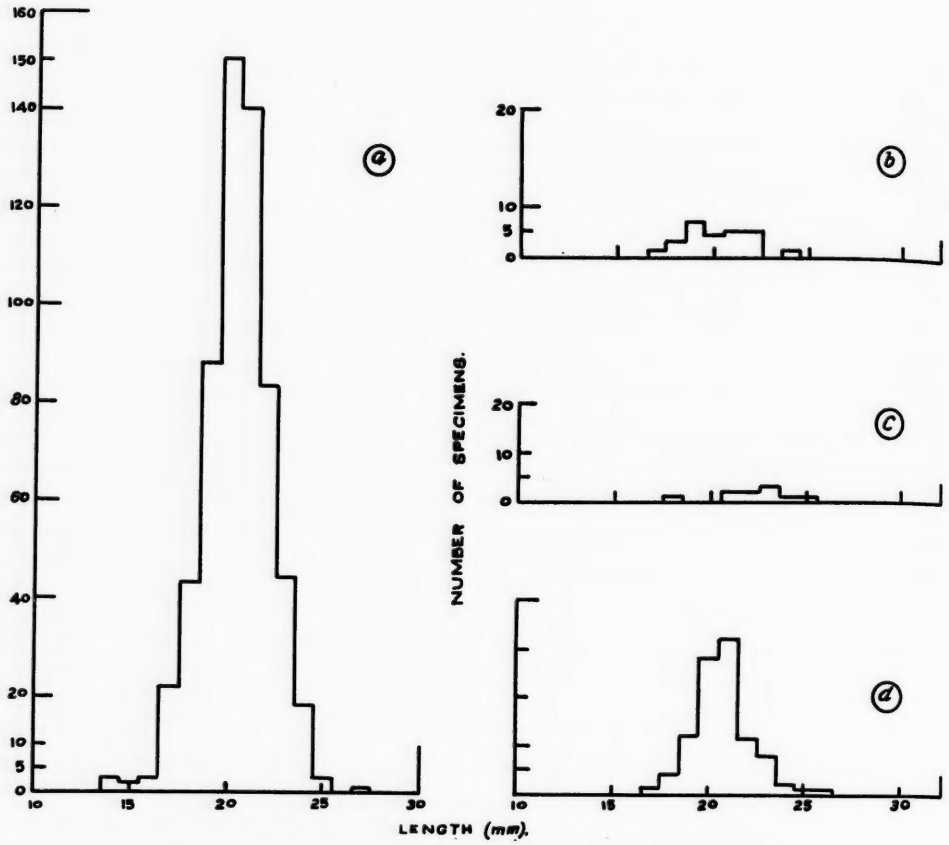
L = Length
W = Width
T = Thickness
CB = Number of costae on brachial valve
CP = Number of costae on pedicle valve
CBF = Number of costae on brachial fold

n = Number of specimens
$\bar{X}$ = Mean
S = Standard deviation
V = Coefficient of variation

Locality	Bio-Character	n	$\bar{X}$	S	100 V
Normandy	L	10	22.2000 ±0.5797	1.8331	8.26
	W	10	25.3000 ±0.6935	2.1932	8.67
	T	10	16.8000 ±0.6754	2,1356	12.71
	100W/L	10	107.20 ±0.2845	0.9000	0.84
	100T/L	10	73.40 ±0.6395	2.0225	2.75
	CB	10	28.4000 ±0.7644	2.4169	8.51
	CP	10	29.5000 ±0.7516	2.3769	8.06
	CBF	10	4.0000 ±0.2448	0.7746	19.36
Langton Herring	L	600	20.4200 ±0.0715	1.7504	8.57
	W	600	21.9267 ±0.0968	2.3700	10.81
	T	600	14.8483 ±0.0909	2.2276	15.00
	100W/L	600	107.43 ±0.0513	1.2564	1.17
	100T/L	600	76.47 ±0.0719	1.7607	2.30
	CB	600	30.1433 ±0.1383	3.3872	11.34
	CP	600	30.9424 ±0.1441	3.5304	11.41
	CBF	600	5.8484 ±0.0395	0.9671	16.54
Burton Bradstock	L	26	20.1154 ±0.3187	1.6249	8.08
	W	26	21.2692 ±0.4268	2.1761	10.23
	T	26	14.5385 ±0.3738	1.9061	13.11
	100W/L	26	103.15 ±0.2661	1.3572	1.31
	100T/L	26	72.54 ±0.3419	1.7435	2.40
	CB	18	29.6667 ±0.5826	2.4719	8.33
	CP	23	30.1739 ±0.3920	1.8802	6.23
	CBF	26	5.5769 ±0.1555	0.7929	14.22
Eype Mouth	L	100	20.7400 ±0.1494	1.4941	7.20
	W	100	22.6400 ±0.2369	2.3686	10.46
	T	100	15.8200 ±0.2080	2.0803	13.15
	100W/L	100	107.82 ±0.1587	1.5867	1.47
	100T/L	100	77.30 ±0.2064	2.0640	2.67
	CB	60	30.3500 ±0.4701	3.6415	12.00
	CP	66	31.4546 ±0.4552	3.6982	11.76
	CBF	100	5.9950 ±0.0964	0.9644	16.09

TABLE 2—COMPARISON OF MEANS

Bio-Character	Normandy Langton Herring	Normandy Burton Bradstock	Normandy Eype Mouth
L_1–L_2	1.7800 ±0.5841	2.0846 ±0.6615	1.4600 ±0.5986
W_1–W_2	3.3733 ±0.7002	4.0308 ±0.8143	2.6600 ±0.7328
T_1–T_2	1.9517 ±0.6815	2.2615 ±0.7719	0.9800 ±0.7067
CB_1–CB_2	−1.7433 ±0.7744	−1.2667 ±0.9609	−1.9500 ±0.8974
CP_1–CP_2	−1.4424 ±0.7653	−0.6739 ±0.8477	−1.9546 ±0.8787
CBF_1–CBF_2	−1.8484 ±0.2480	−1.5769 ±0.2900	−1.9950 ±0.2631
	Langton Herring Burton Bradstock	**Langton Herring Eype Mouth**	**Burton Bradstock Eype Mouth**
L_1–L_2	0.3046 ±0.3267	−0.3200 ±0.1655	−0.6246 ±0.3519
W_1–W_2	0.6565 ±0.4377	−0.7133 ±0.2559	−1.3708 ±0.4881
T_1–T_2	0.3098 ±0.3847	−0.7402 ±0.2272	−1.2815 ±0.4278
CB_1–CB_2	0.4766 ±0.5988	−0.2067 ±0.4900	−0.6833 ±0.7486
CP_1–CP_2	0.7685 ±0.4178	−0.5122 ±0.4775	−1.2807 ±0.6008
CBF_1–CBF_2	0.2715 ±0.1607	−0.1466 ±0.1045	−0.4181 ±0.1831



TEXT-FIG. 2—Frequency histograms of length. (a) Langton Herring, (b) Burton Bradstock, (c) Normandy, (d) Eype Mouth.

comparison of mean values of bio-characters is probably of little taxonomic significance.

FREQUENCY-DISTRIBUTION OF WIDTH /LENGTH AND THICKNESS/LENGTH

The distributions of width/length and thickness/length have been expressed as percentages, and then treated in the same way as the other distributions. The tests (skewness and kurtosis[3]) have shown no departure from normality, t being well below 1% level in each case.

Previously in many quantitative studies, much importance has been given to the means of the ratio-distributions (as a shape parameter). Consequently, they have been used for the purpose of comparisons. In the present instance, there are some significant differences in means of ratio-distributions, but such differences are not considered to be of any taxonomic importance, as the bio-characters themselves demonstrate a considerable degree of correlation and are subjected to allometric and not isometric growth. It is evident, in such a case that the ratios are dependent on size and, therefore, suffer from the same disadvantages as the means of size distributions. This is clearly seen, as in three of the four samples, higher values of the means of ratios are associated with the higher values of the linear variates

[3] Westoll (1950) suggested the possible existence of sexual dimorphism in *Dielasma elongata* on the basis of platykurtic and bimodal thickness/length distribution. His remark that *G. boueti* does not show such dimorphism is confirmed by the present study.

(Table 1). The exception is found in the case of the Normandy collection, where the mean values of length, width and thickness are higher than in any other sample, while the ratios remain the same as the other samples in the case of width/length and even less for thickness/length. Anomalies of this nature may be due to the small size of the sample.

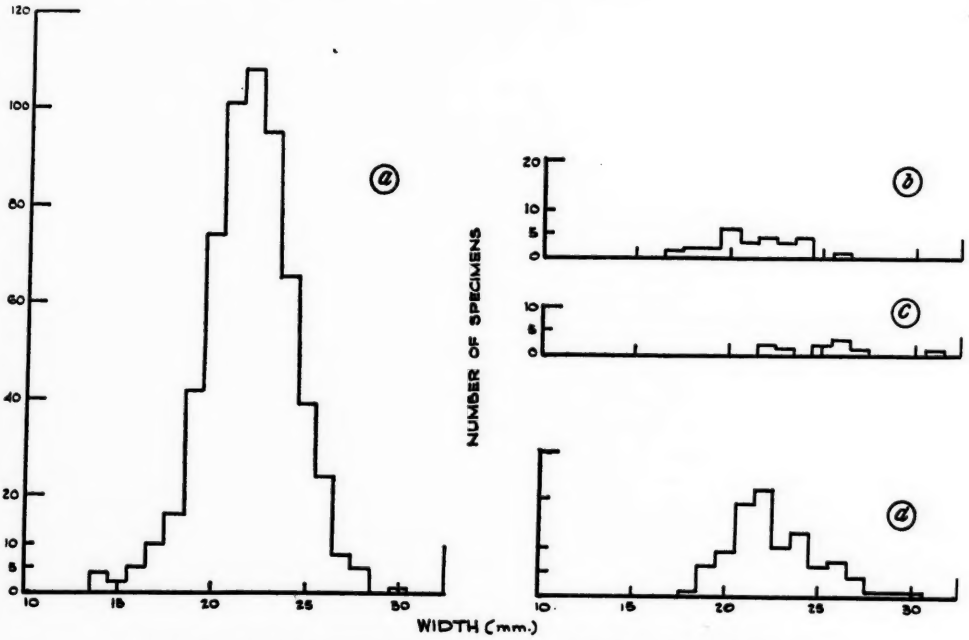
DISTRIBUTION OF COSTAE ON BRACHIAL AND PEDICLE VALVES

The surface ornamentation of *G. boueti* consists of triangular costae radiating from the umbonal regions of the two valves. The ribbing is essentially of a simple nature and no bifurcation has been observed, although the number of costae varies from individual to individual. The simple nature of the ribbing system means that the number of costae in an individual is independent of its size. Differences in the mean number of costae between the collections have been estimated in the conventional way by pooling the standard error of different samples. Parkinson (1954) in a similar case used a chi-square test to compare the rib frequencies between collections. In the present work some of the samples are very small, and this method has not been employed. It is not admissible to use a chi-square test where the cell frequency goes below five, and at least in the case of the Normandy collection most of the cell frequencies would be less than five. In this case, however, a comparison of means is justified since the number of ribs is independent of the size of the individual.

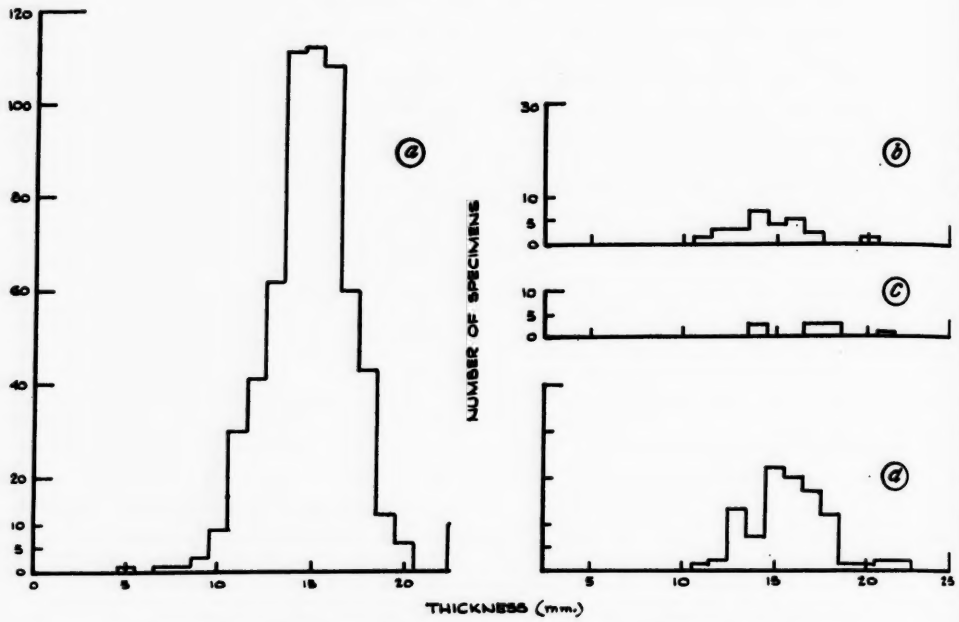
For this analysis it was not possible to use the whole collections, for some specimens are so badly preserved that accurate rib-counts could not be made. The total numbers of individuals used in each case are shown in Table 1.

The arithmetic means of the numbers of costae on the brachial valve are always approximately one less than on the pedicle valve. These observed differences are, however, not statistically significant except in the case of the Langton Herring sample. It is interesting to note that Cumings & Mauck (1902) came across in *Platystrophia lynx* a similar result of one valve having one more rib than the other.

Table 2 contains the result of the comparison of the means of costal distributions.



TEXT-FIG. 3—Frequency histograms of width. (a) Langton Herring, (b) Burton Bradstock, (c) Normandy, (d) Eype Mouth.



TEXT-FIG. 4—Frequency histograms of thickness. (a) Langton Herring, (b) Burton Bradstock, (c) Normandy, (d) Eype Mouth.

The means of the brachial valves do not differ significantly between Langton Herring, Burton Bradstock and Eype Mouth ($P > 0.05$), nor does Normandy with Langton Herring and Eype Mouth ($0.05 > P > 0.02$), nor Normandy with Burton Bradstock. In the case of the pedicle valve, there are no significant differences between any of the collections ($P > 0.05$, except between Eype Mouth and Burton Bradstock, and Normandy $0.05 > P > .02$).

One sees, therefore, that, as regards the mean number of costae, it is not possible to discriminate either the French from the British collections, or the various localities of the latter among themselves.

It may be noted that Davidson (1852) mentioned the occurrence of about thirty ribs on each valve of *G. boueti*. In the Normandy collection the average number of costae on the brachial valve has been found to be 28.40 and 29.5 on the pedicle valve.

DISTRIBUTION OF COSTAE ON FOLD

The average number of costae on the fold of the brachial valve has been compared between collections, the results being shown in Table 2. The mean of the Normandy collection differs significantly from Langton Herring, Burton Bradstock and Eype Mouth ($P < 0.01$), while British collections show no difference within themselves ($P > 0.05$, except Burton Bradstock and Eype Mouth were $0.05 > P > 0.02$): the French forms have four costae on the fold, while the English ones have nearer six.

CORRELATION OF BIO-CHARACTERS

The following two equations have been considered suitable for the study of relative growth of two characters, x and y:

$$1) \quad y = ax + b$$

$$2) \quad y = \beta x^{\alpha}$$

or in log form:

$$\log y = \alpha \log x + \log \beta$$

where a, b, α and β are constants. The first equation is (except for the constant b) the limiting case of the second when $\alpha = 1$, and is often called the isometric growth equation. Strictly speaking, however, it should not be called the equation of isometry unless $b = 0$, as when b differs from zero, the body

proportions are subjected to continuous alteration. The constant α of the second equation has been called by Huxley (1932) the *constant differential growth ratio* and represents the ratio between the relative growth rates of the two characters. As for the constant β, no specific biological significance has been found, but it has been found to be of great advantage in taxonomic problems. Kermack (1954) has considered it to represent the *inherent* or *initial shape* of the organism.

The constants, a, b, α and β may be obtained by fitting a regression line to the arithmetic or logarithmic data by the method of least squares, but the use of regression in this case is open to serious objection. Fitting a regression line assumes that the error of measurement in a sample is all due to the dependent variates. Hence it is a line about which the sum of squares of the dependent variates is minimum. In a biological population, on the other hand, the observed scatter of a bi-variate distribution is not due to errors of measurement but is inherent in the population. Jones (1937) showed that the line

$$\frac{y-\bar{y}}{S_y}=\frac{x-\bar{x}}{S_x}$$

is neutral between the two variates, and is invariant under change of scale. This is known as the *reduced major axis.*

If the fitted reduced major axis straight line does not pass through the origin an allometric relation between the variates may be suspected. (It can be tested also by estimating the standard error of b). Kermack & Haldane (1950) developed a simpler method for the computation of the logarithmic reduced major axis by assuming the logarithms of the distribution to be normal:[4]

$$\alpha=\frac{S_X}{S_Y}$$

where

$$S_X^2=\log(1+V_x^2)$$

and

$$S_Y^2=\log(1+V_y^2)$$

$$\log\beta=\bar{Y}-\tfrac{1}{2}S_Y^2-\alpha(\bar{X}-S_X^2)$$

For the sake of convenience the logarithmic reduced major axis may be called *axis of allometry* (Teissier, 1948, quoted by Haldane 1950).

Table 3 shows the values of different con-

[4] A capital symbol or suffix is used to denote the parameter of logarithmic distribution.

TABLE 3—ORIGINAL DATA

$y=ax+b$

Variates	x / y	Length / Width	Length / Thickness	Width / Thickness
Normandy	*n*	10	10	10
a		1.1964 ± 0.0752	1.1650 ± 0.3251	0.9737 ± 0.2879
b		− 1.2601 ± 1.5471	− 9.0630 ± 7.2516	−7.8346 ± 7.3270
r		0.9800	0.4699	0.3544
Langton Herring	*n*	600	600	600
a		1.3540 ± 0.0332	1.2726 ± 0.0422	0.9399 ± 0.0351
b		− 5.7220 ± 0.6434	−11.1381 ± 0.8616	−5.7606 ± 0.7792
r		0.7904	0.5553	0.4054
Burton Bradstock	*n*	26	26	26
a		1.3392 ± 0.1694	1.1730 ± 0.2008	0.8759 ± 0.1567
b		− 5.6693 ± 3.4252	− 9.0566 ± 4.0484	−4.0912 ± 3.3580
r		0.7635	0.4891	0.4101
Eype Mouth	*n*	100	100	100
a		1.5853 ± 0.1154	1.3923 ± 0.1391	0.8783 ± 0.0847
b		−10.2391 ± 2.4202	−13.0563 ± 2.8839	−4.0647 ± 1.9334
r		0.6828	0.1104	0.2557

TABLE 4—LOGARITHMIC DATA (Natural logs)

$\log y = \alpha \log x + \log \beta$

Variate	e^x / e^y	Length / Width	Length / Thickness	Width / Thickness
Normandy	n	10	10	10
	α	1.0503 ± 0.0622	1.5356 ± 0.4278	1.4621 ± 0.4281
	$\log \beta$	−0.0253 ± 0.2669	−1.9420 ± 1.7091	−1.9047 ± 1.6304
	$\dot{r}$	0.9825	0.4729	0.3779
Langton Herring	n	600	600	600
	α	1.2646 ± 0.0358	1.7461 ± 0.0580	1.3831 ± 0.0517
	$\log \beta$	−0.7283 ± 0.1219	−2.5741 ± 0.2235	−1.5759 ± 0.1877
	$\dot{r}$	0.8113	0.5562	0.4104
Burton Bradstock	n	26	26	26
	α	1.2651 ± 0.1491	1.6189 ± 0.2757	1.2800 ± 0.2282
	$\log \beta$	−0.7412 ± 0.6017	−2.1859 ± 1.0155	−1.2388 ± 1.3472
	$\dot{r}$	0.7997	0.4946	0.4146
Eype Mouth	n	100	100	100
	α	1.4459 ± 0.1032	1.8187 ± 0.1817	1.2579 ± 0.1213
	$\log \beta$	−1.2660 ± 0.4089	−2.7571 ± 0.5811	−1.1649 ± 0.4270
	$\dot{r}$	0.6986	0.1128	0.2564

stants of the fitted reduced major axis, while Table 4 shows the values of the axis of allometry. The constants have been assigned by considering first length as x and width and thickness as y, and then width as x and thickness as y. The coefficient of correlation has been computed for each sample, in both cases as linear (r) and as curvilinear functions ($\dot{r}$). An interesting feature is the slight but distinct increase in the estimated values of correlation coefficient when logarithmic data are used.

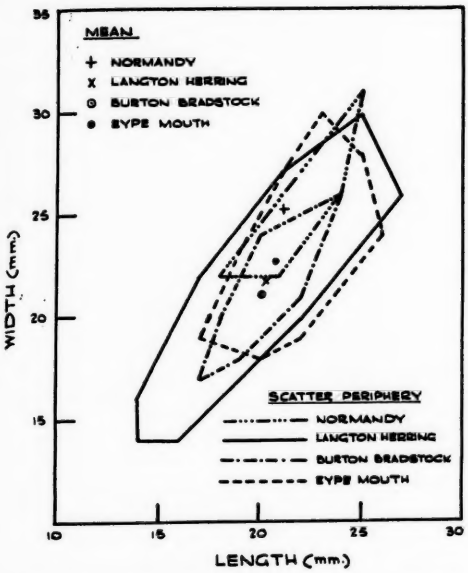
Normandy: In all cases (length × width, length × thickness and width × thickness) the allometric growth rates (α) do not show significant departures from unity ($P > 0.05$), nor the intercepts of the linear function (β) from zero ($P > 0.05$). Failure to show allometric growth is most likely due to the smallness of the sample.

Burton Bradstock: Growth features of the Burton Bradstock collection are very similar to Normandy (from a biological point of view) while the values of constants themselves are more like those of Langton Herring. α does not depart significantly from unity ($P > 0.05$, except for length × thickness $0.05 > P > 0.02$). The value of the intercept b is also not significant ($P > 0.05$ and $0.05 > P > 0.02$ in respective cases).

Langton Herring: In contrast with the Normandy and Burton Bradstock collections, the Langton Herring sample shows marked allometric relations between all bio-characters. The constant differential growth ratio in each case is significantly different from unity ($P < 0.01$), and the intercept b is also significant ($P < 0.01$).

Eype Mouth: Here again marked allometric relations are shown between all the biocharacters, the values of α being significant ($P < 0.01$ except in the case of length × thickness $0.05 > P > 0.02$). The intercepts b are also significant.

From the biological point of view the results of the Langton Herring and Eype Mouth samples show that the animals became more globose and wider with increase in length. The interrelations of the biocharacters in fact suggest continual changes of shape with increase in age. It has been noticed that the variation in shell-shape of individuals depends mainly upon the position of the maximum width. A specimen having maximum width near the anterior margin will show a somewhat triangular shape, whereas a specimen whose maximum width lies nearer the centre will appear almost semicircular. Here it is seen that the width has a faster growth rate than the



TEXT-FIG. 5—Superimposed scatter-peripheries of length×width.

length. With the increased growth rate not only does the shell become wider but also the position of the maximum width migrates, probably for proper adjustment. An individual which started off with an almost semicircular shell-shape turns into a triangular form at a later stage in its life. This change in shell-shape may be demonstrated also on individual shells, for the earlier growth lines are semicircular, while the final shape of the shell is triangular.

From Table 4 it may be seen that the values of correlation coefficient of length ×thickness are much lower than length ×width. Mitra (1957) with the help of longitudinal sections along the plane of symmetry of the shell has shown that animals having the same length may have very different values of thickness. As a result, the observed scatter of length×thickness (text-fig. 6) is much wider than that of length ×width (text-fig. 5), and the length×thickness correlation coefficient is low in all samples.

VARIATION BETWEEN THE COLLECTIONS

The samples from the four localities may now be compared on the basis of the parameters derived from them.

TABLE 5—COMPARISON OF SHAPE AND GROWTH RATE

Length×Width

Parameters	Normandy Langton Herring	Normandy Burton Bradstock	Normandy Eype Mouth	Langton Herring Burton Bradstock	Langton Herring Eype Mouth	Burton Bradstock Eype Mouth
$(M_{X,1}-M_{Y,1})^*$ $-(M_{X,2}-M_{Y,2})$	-0.0605 ± 0.0075	-0.0757 ± 0.0141	-0.0444 ± 0.0102	-0.0152 ± 0.0125	0.0161 ± 0.0079	0.0313 ± 0.0143
$\alpha_1-\alpha_2$	-0.2143 ± 0.0721	-0.2148 ± 0.1615	-0.3956 ± 0.1204	-0.0005 ± 0.1533	-0.1813 ± 0.1091	-0.1806 ± 0.1811
$\dot{\alpha}$	—	—	—	1.2638 ± 0.0412	1.2857 ± 0.0346	1.3872 ± 0.0781
$\log \dot{\beta}_1 - \log \dot{\beta}_2$	—	—	—	0.0114 ± 0.0616	-0.0113 ± 0.0330	-0.0192 ± 0.0721
$\log \beta_1 - \log \beta_2$	0.0394 ± 0.0025	0.0507 ± 0.0145	0.0157 ± 0.0069	—	—	—

* $M_X - M_Y$ Normandy -0.1294 ± 0.0071 Langton Herring -0.0689 ± 0.0026 Burton Bradstock -0.0537 ± 0.0122 Eype Mouth -0.0850 ± 0.0074

TABLE 6—COMPARISON OF SHAPE AND GROWTH RATE
Length × Thickness

Parameters	Normandy Langton Herring	Normandy Burton Bradstock	Normandy Eype Mouth	Langton Herring Burton Bradstock	Langton Herring Eype Mouth	Burton Bradstock Eype Mouth
$(M_{X,1}-M_{Y,1})^*$ $-(M_{X,2}-M_{Y,2})$	-0.0477 ± 0.0364	-0.0468 ± 0.0424	0.0065 ± 0.0384	0.0009 ± 0.0229	0.0542 ± 0.0150	0.0533 ± 0.0265
$\alpha_1-\alpha_2$	-0.2105 ± 0.4318	-0.0833 ± 0.5090	-0.2831 ± 0.4648	0.1272 ± 0.2818	-0.0726 ± 0.1908	-0.1998 ± 0.3302
$\dot{\alpha}$	1.7419 ± 0.0566	1.5942 ± 0.2317	1.7755 ± 0.1667	1.7405 ± 0.0574	1.7527 ± 0.0548	1.7578 ± 0.1513
$\log \dot{\beta}_1 - \log \dot{\beta}_2$	-0.0145 ± 0.1212	-0.1166 ± 0.1526	-0.0584 ± 0.1334	-0.0116 ± 0.0748	-0.0415 ± 0.0414	-0.0296 ± 0.0865
$\log \beta_1 - \log \beta_2$	—	—	—	—	—	—

*	Normandy	Langton Herring	Burton Bradstock	Eype Mouth
$M_X - M_Y$	0.2832 ± 0.0361	0.3309 ± 0.0050	0.3300 ± 0.0224	0.2767 ± 0.0141

TABLE 7—COMPARISON OF SHAPE AND GROWTH RATE
Width × Thickness

Parameters	Normandy Langton Herring	Normandy Burton Bradstock	Normandy Eype Mouth	Langton Herring Burton Bradstock	Langton Herring Eype Mouth	Burton Bradstock Eype Mouth
$(M_{X,1}-M_{Y,1})^*$ $-(M_{X,2}-M_{Y,2})$	0.0128 ± 0.0391	0.0289 ± 0.0458	0.0509 ± 0.0412	0.0161 ± 0.0252	0.0381 ± 0.0153	0.0220 ± 0.0283
$\alpha_1-\alpha_2$	0.0790 ± 0.4313	0.1821 ± 0.4852	0.2042 ± 0.4450	0.1031 ± 0.2339	0.1252 ± 0.1319	0.0221 ± 0.2585
$\dot{\alpha}$	1.3839 ± 0.0520	1.3203 ± 0.2010	1.2732 ± 0.1166	1.3784 ± 0.0510	1.3621 ± 0.0480	1.2620 ± 0.1095
$\log \dot{\beta}_1 - \log \beta_2$	-0.0682 ± 0.1141	-0.0846 ± 0.1556	-0.0813 ± 0.1200	-0.0274 ± 0.0764	-0.0261 ± 0.0429	0.0056 ± 0.0849
$\log \beta_1 - \log \beta_2$	—	—	—	—	—	—

*	Normandy	Langton Herring	Burton Bradstock	Eype Mouth
$M_X - M_Y$	0.4126 ± 0.0384	0.3998 ± 0.0058	0.3837 ± 0.0245	0.3617 ± 0.0141

It has been mentioned before that the use of size parameters (e.g., the means of biocharacters etc.) as a basis for comparison is useless as they are subjected to various secondary alterations. Nor is the comparison of means of ratios any better, as the ratios themselves are dependent on size. Shape parameters are more suitable in such cases and furnish more correct conclusions. The methods used here are essentially those of Kermack & Haldane (1950), as further developed by Kermack (1954).

The following parameters have been compared by t-test, after the estimation of suitable sampling variance. They are: (a) *average shape* (see below) (b) *constant differential growth rate* (α) and (c) *inherent shape* ($\log \beta$). The average shape is the logarithm of the ratio of the geometric means (m_X and m_Y) of the two characters. Standard error of $m_X - m_Y$:

$$\left[\frac{S_Y^2 + S_X^2 - 2S_X S_Y r}{n}\right]^{1/2}$$

Perhaps the best parameter for comparison is the inherent shape ($\log \beta$) where alterations of shape due to allometric growth are eliminated. Estimation of this is carried out in two stages. Firstly the two values of α are compared, and if these do not differ significantly the α's from the two samples are pooled ($\dot{\alpha}$). From the pooled $\dot{\alpha}$, the respective inherent shapes:

$$\log \dot{\beta}_1 = M_{Y,1} - \dot{\alpha} M_{X,1}$$
$$\log \dot{\beta}_2 = M_{Y,2} - \dot{\alpha} M_{X,2}$$

are estimated. These may be compared with the help of the standard error of their differences:

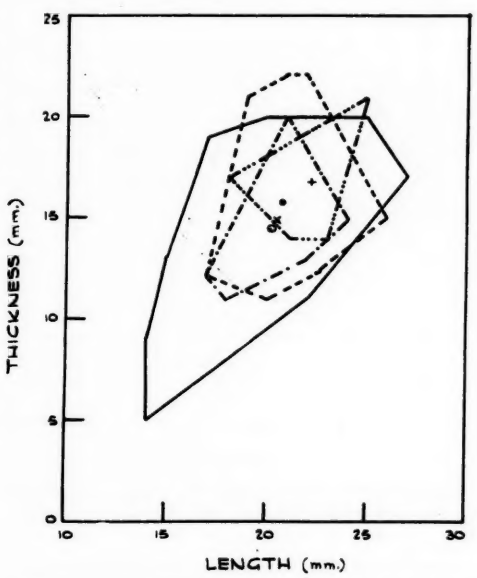
$$\left[\frac{S_{Y1,}^2 + \dot{\alpha} S_{X,1} - 2\dot{\alpha} S_{X,1} S_{Y,1} r_1}{n_1} + \frac{S_{Y2,}^2 + \dot{\alpha} S_{X,2} - 2\dot{\alpha} S_{X,2} S_{Y,2} r_2}{n_2} + (m_{X,1} - m_{X,2})\ \mathrm{Var}\ \dot{\alpha}\right]^{1/2}$$

When, however, the α's do differ the $\log \beta$'s at m_X Normandy have been compared. This is necessary because $\log \beta$ is a parameter having values depending on the values of x chosen. The most accurate estimation of $\log \beta$ is therefore at maximum values of the size parameter (Kermack, loc. cit.).

Standard error of $\log \beta_1 - \log \beta_2$:

$$\left[\frac{S_{Y1,}^2 (1 - r_1^2)(\dot{X} - m_{X,1})^2}{n_1 S_{X1,}^2} + \frac{S_{Y2,}^2 (1 - r_2^2)(\dot{X} - m_{X,2})^2}{n_2 S_{X2,}^2}\right]^{1/2}$$

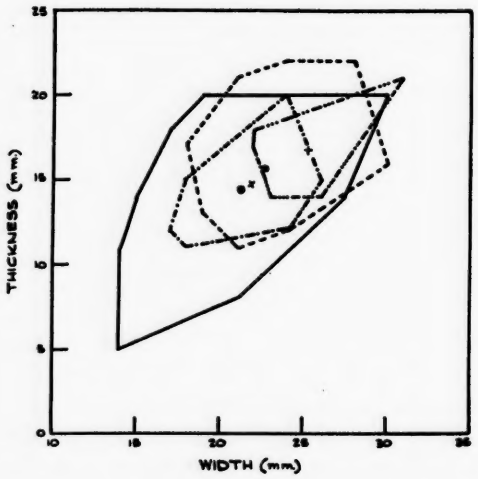
where $\dot{X} = m_{X\ \mathrm{Normandy}}$



TEXT-FIG. *6*—Superimposed scatter-peripheries of length × thickness. Symbols as in text-fig. 5.

Length × width. The average shape between length and width of the Normandy collection differs significantly from all the British collections ($P > 0.01$), but the British collections do not differ among themselves ($P > 0.02$ in each case). Similarly the constant differential growth ratio (α) shows significant differences between the French and the British collections ($P > 0.01$ except between Burton Bradstock and Normandy $P > 0.05$), while the British collections again do not differ among themselves ($P > 0.05$). The Burton Bradstock collection is very small, and the absence of significant difference in α from the Normandy collection is probably due to its small size. For practical purposes the Burton Bradstock collection may be pooled with that from Langton Herring in which case the French sample differs from all the British collections.

As α differs significantly between the



TEXT-FIG. 7—Superimposed scatter-peripheries of width×thickness. Symbols as in text-fig. 5.

British and the French collections, the inherent shapes (log β) have been estimated at m_X Normandy. Normandy log β at m_X Normandy shows a significant difference from all the British collections ($P < 0.01$). As α within the British collections do not differ, they have been pooled and the estimated values of log β do not show any differences ($P > 0.05$).

Length×Thickness. The average shapes do not differ between any collections ($P > 0.02$) except between Langton Herring and Eype Mouth ($P > 0.01$). The constant differential growth ratios do not differ significantly between any of the collections. Log $\dot{\beta}$ has been estimated from the pooled $\dot{\alpha}$ and these also do not differ significantly; in fact, the observed difference in each case is less than their standard error.

Width×Thickness. In this respect, neither the average shapes, nor constant differential growth ratios nor the inherent shapes differ between any of the collections. The observed difference in each case is less than the standard error.

TAXONOMY AND ECOLOGY

The fact that in all the collections the frequency distributions of the different biocharacters are unimodal suggests that each cllection is homogeneous, and in fact none of the methods used has provided any basis for splitting up the individual collections.

The comparison of shape parameters shows that length and width correlation provides the best discriminating factor between the collections. If we discriminate on this basis (length×width) we can regard all the British collections as having been drawn from the same population,[5] while the French forms constitute a biometrically separate population, having a lower growth ratio (α), a lower inherent shape (log β) and a higher average shape. Biologically this means that the French forms have grown faster in width relative to length, and have a relatively wider shell shape.

The number of ribs on the sulcus provides another basis for discrimination between populations which agrees with that provided by length×width correlations: the French forms have four ribs on the sulcus, while all the British collections have nearly six.

Ecological studies on living brachiopods suggest that variation in shell shape may be dependent on variation in the nature of the substratum to which the animal is attached (Du Bois 1916, Percival 1944). It is possible, therefore, that the observed differences in shell shape between the French and the British forms of *G. boueti* may be due mainly to the influence of the environment, and do not necessarily reflect derivation from two different genetic stocks. All the collections are considered provisionally to belong to one species.

Subdivision of the collections is to some extent arbitrary. (It depends for instance on which character is chosen as the discriminating character). The Normandy specimens, however, differ significantly from all the British forms in many of their parameters (particularly of length×width), and it seems appropriate to regard these specimens as a subspecies (the nominate subspecies) distinct from that represented by the British form. The slight difference (length×thickness average shape) between

[5] The only character on which it is possible to discriminate between the British collections is length×thickness average shape, of which the difference between Langton Herring and Eype Mouth is significant. The lack of significant differences in the other characters, however, is considered taxonomically to outweigh this factor.

the British forms from Langton Herring and Eype Mouth is considered to be intra-subspecific variation.

Davidson's (1878) lumping of the French and the British forms together is not, therefore, accepted; nor, on the basis of the characters studied in the present investigation, is there any evidence to support Buckman's (1917) splitting of the latter into two species (one at Burton Bradstock and the other at Eype Mouth). Accordingly the collections are grouped into one species *G. boueti* Davidson; and this species is subdivided into two subspecies *G. boueti boueti* Davidson from Normandy and *G. boueti goniaea*[6] Buckman (with synonym *G. boueti contracta* Buckman) from the Dorset localities.

From Table 4 it may be seen that several of the parameters have a graded westward trend from Normandy to Eype Mouth. The growth ratio (α) gradually increases westward in the case of length×width, and gradually decreases for width×thickness. (The length×thickness character gradient is not so obvious as the Burton Bradstock's value is irregular.) The inherent shape ($\log \beta$) also shows a westward trend, as does the width×thickness average shape. These results suggest comparison with the concept of the *Cline*, introduced by Huxley (1938). But although this comparison is suggestive, it should be emphasized that differences between the parameters of the British specimens are in general not significant and the trends of their values may be due to sampling error.

In a variation study such as the present the designation of a single type specimen (in the present case it would be a lectotype) is considered inappropriate. The author recommends, however, the concept of the *hypodigm* of Simpson (1940) as revised by Newell (1949). The British Museum (Natural History) collection of *G. boueti boueti* from Normandy (Registered numbers B. 5512), and the author's collection from Eype Mouth, together with Buckman's original specimen (the original locality of *goniaea*), may be considered the nuclei of the hypodigms of the two subspecies.

[6] The name *goniaea* has page and line priority over *contracta*.

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JOURNAL OF PALEONTOLOGY, V. 32, NO. 5, P. 1007–1009, 2 TEXT-FIGS., SEPTEMBER 1958

FREQUENCY CURVES AND DEATH RELATIONSHIPS AMONG FOSSILS

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ABSTRACT—Size-frequency curves have been used to determine life and death relationships among organisms. By plotting a normal growth rate curve over a series of typical survivorship curves for invertebrates, skewed and normal distribution curves result. A bell curve of size-frequency may result from normal life activities or from posthumous sorting. Other methods of analysis must be used to differentiate sorted and unsorted populations.

INTRODUCTION

IT HAS become common practice during recent years to show graphically variation within taxonomic units. Histograms and frequency curves or scatter-grams of length, width, thickness, or other morphologic characteristics are the rule in paleontologic papers rather than the exception when more than a few specimens are involved in a collection. These graphs and histograms have been of considerable interest in terms of ecologic interpretation. Work by Boucot (1953), Tasch (1953), Cloud (1948), and many others have substantiated the usefulness of such graphs for postulating past conditions.

OBSERVATIONS

Graphs of rate of growth or of size of a morphologic character on one individual through time show a characteristic S-shaped curve, asymptotic for a short time in the early embryonic and early juvenile stage followed by a rapid increase in slope during juvenile and early adult stages and becoming again asymptotic in gerontic stages of growth. In fossil populations one would anticipate only shells representative of the steep and later asymptotic portions of the curve.

Few invertebrates have been studied over a sufficiently long period of time for data to be gathered concerning their annual size increase or growth rate. Oysters, referred to by Deevey (1947) and Thompson (1948) seem to represent a characteristic group of invertebrates and will be considered typical of shelled invertebrates in the present discussion.

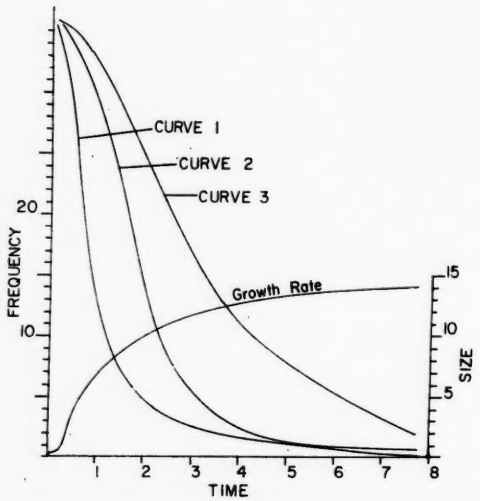
A growth curve shown by Thompson (1948, p. 166) extends over an eight year period with the initial embryonic and early juvenile stages postulated but unobserved. The documented history of the oyster begins with the steeply rising growth stage after the shell had already reached a width of 50 mm., approximately eight or nine months old. The curve is convex upward, and approaches an asymptotic condition in the later years, but even after eight years the animal was evidently still increasing in size, but at a very slow rate.

A similar pattern of growth is probably characteristic of other invertebrates. The placement and development of growth lines in brachiopod, gastropod, and cephalopod shells, of the diaphragms in bryozoans, and tabulae and growth lines in rugose corals indicate a similar rate of growth.

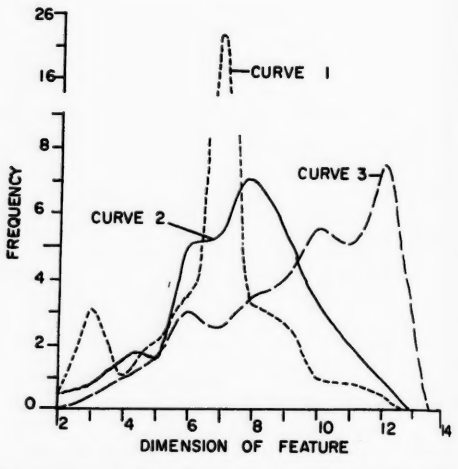
In terms of size-frequency of morphologic features, we find other systematic influences upon what the final distribution will be. Ruling out, for the time being, such post-death factors as current sorting, scavengers, and selective preservation, we find the effect of mortality rate as significant in determining the ultimate frequency of shells of a given size from a given population.

Deevey (1947, p. 312) has inferred a survivorship curve for oysters, and Percival (1944) has observed frequency distribution of brachiopod sizes. Both produce essentially the same type of curve, concave upward, with a steep initial part, but gradually becoming nearly asymptotic for the larger sizes. Other curves of similar nature have been prepared by Boucot (1953), Tasch (1953) and many other paleontologists.

By combining the growth curve and the survivorship curve we can deduce the char-



TEXT-FIG. *1*—Characteristic rate of growth curve and three representative mortality curves for shelled invertebrates.



TEXT-FIG. *2*—Size frequency curves for populations shown in text-fig. 1, indicating distribution of size of morphologic feature after entire population has died with each of the three rates of mortality.

acteristics of dead shells which will accumulate in the area occupied by a species. Three different survivorship curves have been plotted over a growth rate curve considered typical of invertebrates in text-fig. 1. By noting the number of individuals which die during each unit increase in size on the growth curve, we can obtain an estimate as to the size frequency to be expected. Table 1 shows the number of shells expected for each size class from one set or population, using mortality curve 2 and the growth curve as plotted.

TABLE 1—FREQUENCY OF SHELL SIZE ANTICIPATED IN POPULATION WITH ASSUMED GROWTH RATE AND SURVIVORSHIP CURVE #2 OF TEXT-FIG. 1

Class Interval	Frequency
1	0
2	0.5
3	1.0
4	4.5
5	2.0
6	2.0
7	5.0
8	5.5
9	5.5
10	3.5
11	2.0
12	1.0
13	1.0
14	1.0

It is evident from Table 1 and from text-fig. 2 that by varying the mortality rate and keeping the growth rate constant, or the reverse, we can produce curves of various types. With the assumed growth rate, curve 2 produces a nearly symmetrical bell curve. With a variation in mortality as in curve 3, we produce a curve skewed strongly to the right. The mortality rate must have been very great, practically instantaneous, to produce the strongly left skewed curves of fossil groups discussed by Boucot (1953, p. 34–39) or Tasch (1957, p. 376). A strongly grouped curve results from the relationship of the assumed mortality curve 1 and the growth rate curve of text-fig. 1.

It is evident that if the curve of shell size-frequency is similar to that of a mortality or survivorship curve that the entire population was killed catastrophically. On the other hand, a size-frequency curve approaching that of a bell curve may result either from continual occupancy of the area by the species in question or from the shells having been sorted after death just as other particles of sediment are sorted. Abrasion, separation of the valves, etc., would then be the most reliable indicators of posthumous sorting. It is thus possible, with some caution, to differentiate a fossil population which died catastrophically from one which

resulted from continual occupancy of an area, and from one which has been secondarily sorted. The term biocoenosis could well apply to the first as proposed by other workers, thanatocoenosis to the second, and necrocoenosis to the third.

Duration of occupancy of any particular species should be indicated by abundance and density within the sample. Ratios of length of occupation could be established by comparing ratios of modal and flank regions of the curves, with curves of other samples. Only relative time could ever be determined even under ideal conditions. Long occupancy of an area would tend to exaggerate the modal area of the curve above the flank areas.

ACKNOWLEDGMENTS

The concept of the importance of mortality and growth rates developed from discussions with graduate students at Brigham Young University. Dr. H. J. Bissell kindly read the manuscript.

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JOURNAL OF PALEONTOLOGY, V. 32, NO. 5, P. 1010–1018, 1 TEXT-FIG., SEPTEMBER 1958

PRESIDENTIAL ADDRESS

THE SCIENCE OF PALEONTOLOGY*

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In presenting the subjoined address for publication I have made no major changes but have added a few words here and there which appear in brackets. At the end, however, I have made some references, some notes, and a few remarks commenting on points in the speech. One of my colleagues felt that I was not fair to a group of stratigraphers who feel that they must describe their fossils. At the appropriate place I discuss this point a little further and hope that I prove fair and am understood.

My purpose in giving this speech in the first place was to make my colleagues aware of the need for revivifying Paleontology and to point out the problems connected with such a rejuvenation. In all branches of science fads arise that divert many from the main channel of study. This is especially true in Paleontology, and I am most hopeful that the mainstream of Paleontology, taxonomy and morphology, can be kept flowing.

As PRESIDENT of your Society I have taken the liberty of reviving the annual address. It seems to me that each year your president should have a message for you. In Paleontology we have many problems, not only scientific ones, but problems that involve our very existence as a society and a Science. Now that the custom has been renewed, I hope that future presidents will have the desire to talk over affairs with you.

The problem I want to discuss today concerns a trend in Paleontology, especially Invertebrate Paleontology, that alarms me considerably.[1] This is the decline of what I shall call pure or "old-fashiond" Paleontology. This decline started in the great blossoming of stratigraphy that has taken place in the last few decades. With the rise of stratigraphy a decline in Invertebrate Paleontology is evident. The wane of the descriptive, taxonomic, and morphological phases bothers me because I think that this decline may ultimately dry up the main stream of Paleontology. I am expressing my views in the hope that some of you will look at the problem as I do, with alarm and the desire to revive Paleontology.

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As a test for my point of view I quizzed some of my colleagues on the numbers of expert paleontologists available in the United States in the various fossil invertebrate groups.[2] I asked to whom they would turn for help in graptolites, bryozoans or other phyla. The sort of experts I have in mind are men who have mastered the details of a whole group.[3] The questioning indicates clearly that we have few masters in our country today. Let me cite examples: in Porifera we have one; in corals one definitely, possibly three more; in worms, none; in Bryozoa, two, but one has been long in retirement; in brachiopods two; in echinoderms in general, none, but in various branches of them, such as echinoids, two; crinoids one; cystoids two; blastoids one; starfishes none; in gastropods we have no one who has mastered the entire group, but in the Paleozoic we have one (now retired), in the Mesozoic, none, and in the Tertiary, one; in pelecypods, one in the Paleozoic, none in the Mesozoic and one or two in the Tertiary. We are richer in cephalopod workers with four in the Paleozoic, and three on special groups in the Mesozoic. Coverage in the Arthropods is again on the modest side: one in post-Cambrian trilobites two in Cambrian trilobites; one in Arachnida; one in insects; one in crabs and lobsters; and one in the less common groups of arthropods.[4] We have only one worker left in graptolites, an old stalwart of 90 years.[5] I purposely left out micropaleontology because it is more adequately staffed. But even there, we have few who are broadly expert.

In the biological sciences the descriptive and taxonomic phases are also in decline even though the exploration of the ocean and lands is far from complete. Nor is modern classification of animals now completely settled. In the 1953 report of the Society of Systematic Zoology the same gloomy picture seen in Paleontology was painted for Recent invertebrates by Dr. Fenner Chace, but with the difference that his canvas covered

the whole world.[6] He cited each group of Invertebrates with the number of experts at work on them. The figures are shockingly low. Although so much remains to be done, young men of vision are not enticed into these fields.

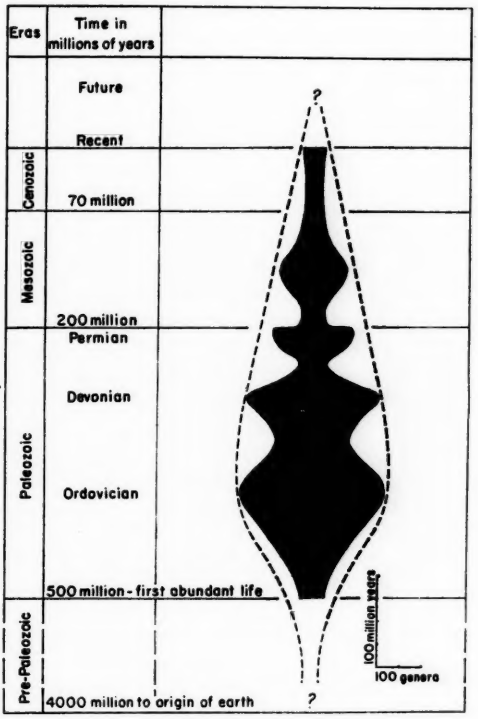
I think eight factors conspire to limit the appeal of pure paleontology and even general zoology to the younger generation. The trends I have in mind are partly inherent in the subject, but others are compounded of the complications of modern life and the dual role Paleontology plays with Stratigraphy:

1) Paleontology is not a popular subject because it has limited practical and economic value. It is generally regarded as a branch of geology which is low man on the scientific totem pole. Geology to date has been slow to achieve recognition by the public, armed services and educators.[7] The waning interest in Paleontology is shown by the fact that one of our leading journals of science will not accept papers on morphology or taxonomy because they are not of "general interest." I might also point to the very modest program following this talk.[8]

2) Paleontology is frightfully complicated [and has an unorganized literature]. It covers all of the life procession, for all time, for the whole world.[9] It is thus a fantastically broad and complicated subject. The detail and collateral subjects that must be mastered limit its appeal. A natural result of the host of facts to be learned is leading to an unfortunate lengthening of the time required to take the Ph.D., a discouragement to young men.

3) Teaching of Paleontology is commonly faulty. Inasmuch as the subject is often taught with stratigraphy, or by a stratigrapher,[10] the practical side is stressed, which for Science, is the least rewarding emphasis. Knowledge of fossils as a goal in itself must be the aim in teaching paleontology. Another factor adversely affecting teaching is the general lack of comprehensive collections in most universities. The only true text in Paleontology is the fossils themselves.

4) Divisive forces within paleontology have tended to destroy its unity. The defection of small groups and the rise of micropaleontology have fragmented a society that should continue to embrace everyone interested in fossils. The idea that the small or "micro" fossils of various kinds can be formed into a cohesive science because of their economic value has been an outgrowth unfortunate for paleontology. The contribution of this group at present seems greater to stratigraphy than to paleontology as a whole. The rise of micropaleontology due partly to the attractive initial salaries offered its practitioners and the technical needs of industry has led to a serious neglect of many fossil groups and an imbalance in paleontology.[11]



TEXT-FIG. 1—Spindle diagram showing the range of the brachiopods through geological time. Note the reentrants at the Silurian, Mississippian and Pennsylvanian in the Paleozoic and at the Triassic in the Mesozoic. These are thought to represent gaps in knowledge due to insufficient work on the brachiopods of the Silurian, Mississippian, Pennsylvanian and Triassic.

5) Another factor retarding paleontology, in my opinion, is the idea in exploratory organizations that paleontology is a service to the field man. The paleontologists are generally so loaded with routine that no

time is available for the research needed to keep the subject alive and healthy. It also gives the field man and stratigrapher the idea that the paleontologist is working for them alone; that paleontology, to justify its existence, must be beamed toward stratigraphy.

6) Poor research standards is one of the important factors for the low esteem in which paleontology is held. Some workers publish papers with brief descriptions, poor illustrations of inadequately prepared specimens and without lucid conclusions. At the same time others slave over their fossils, spending weeks merely in preparation of specimens and illustrations. They find competition with workers of low standards difficult indeed.

7) Modern paleontology requires much time for good results. At best it is a painstaking and time-consuming subject; reliable results are no longer quickly possible. Fossils must be prepared preferably by the paleontologist himself. The vertebrate paleontologist is accustomed to the need for arduous preparation, but the stratigraphic [invertebrate] paleontologist is not always willing to give the necessary time to his fossils. Another factor slowing down research is the exhaustive hunt in the [unorganized] literature for facts and figures relating to problems in hand. Still more time-consuming are the necessary legal deliberations required in any taxonomic work dealing with species, genera, and now families. The turmoil introduced by an International Code of Nomenclature in constant flux and the present dubious status of the law of priority are factors limiting the appeal of taxonomic paleontology to impressionable neophytes.

8) Last but not least are the present economic conditions. It is an anomally that in the midst of a fabulous plenty, and when a recent war demonstrated the dependence of our existence on science, salary lag has caused a steady and alarming depletion in the number of all kinds of scientists.[12] Efforts are now being made to rectify this situation but this meritorious action has not reached down to the geologists and paleontologists. In the U. S. Civil Service physicists, chemists and engineers are now enjoying a favored status. They are hired at one grade (about $1000) higher than geologists and biologists.[13]

Some of these trends inimical to interest in paleontology can be overcome, but the difficulties inherent in the subject, such as its scope and specialization, must be borne philosophically. Let us examine paleontology, its component disciplines and its relationship to stratigraphy.

Paleontology is the study of the life of past geological ages. Paleontologists are thus students of fossils. Not long ago a brief but indecisive controversy raged as to whether or not paleontology is more closely allied to geology or zoology.[14] It is obvious that a knowledge of geology is necessary to a study of fossils. It is equally evident that if the chain of life has been unbroken from its beginning, as we believe, the study of fossils is in reality a phase of zoology. More and more the modern paleontologist is turning to Recent animals and environments to find counterparts and conditions that may have obtained in the past when his fossils were living creatures. I am not here reopening this problem because I accept the fact that all life is related and that paleontology is in reality paleobiology, an independent science.[15] Thus I regard the component disciplines of paleontology to be: 1) Morphology, the very foundation of paleontology. 2) From this follows taxonomy or the classification of animals. 3) Evolution or the descent of fossil animals to the Recent logically follows the two preceding. 4) Distribution of fossils in space is a neglected field but their arrangement in time has received much attention. 5) Paleoecology, a subject that has presently come to the front. The [two] recent monographs summarizing Paleoecology show what a vast amount of study has been given it [in a short time]. 6) To the above I add Correlation. Some, no doubt, will feel inclined to debate this because correlation is regarded as a function of stratigraphy. Inasmuch as correlation concerns fossils, faunas and floras, the stuff of paleontology, I believe it to be primarily a function of paleontology, not stratigraphy.[16]

Paleontology and stratigraphy have long been wedded. The association is so close that, in appraising the work of colleagues, past and present, it is often difficult to say whether a man is a paleontologist or a

stratigrapher. The two can be separated, however, by the emphasis and aim of their work, whether the goal is one of knowledge of the physical sequence or whether emphasis is on fossils and problems connected with them.

Grabau emphasizes the physical character of stratigraphy, which he defines as the "inorganic side of Historical geology, or the development through successive geologic ages of the earth's rocky framework or lithosphere."[17] Stratigraphy was recently divided into two parts: lithostratigraphy and biostratigraphy.[18] The former is now a growing and complicated subject. No longer can the mere [biological] paleontologist expect to perform good physical stratigraphy, which is a separate science. Biostratigraphy is concerned, according to a leading textbook, with morphology, properties of assemblages, classification of organisms, biological processes, correlation and evolution.[19] This broad definition includes all the disciplines of paleontology just mentioned. I object to the idea that paleontology is thus merely a branch of stratigraphy because the intricacies of both subjects give any worker more than he can do in either branch without attempting both. That paleontology is a subject of high specialization is evident because the field mapper or physical stratigrapher must have paleontologists to assist him.[20]

As these sciences evolve, becoming more and more complicated, a question arises in my mind as to whether or not the stratigrapher should attempt identification and description of fossils, or whether the paleontologist is qualified to perform physical stratigraphy.[21]

Accuracy demands the best possible effort of the paleontologist in morphological work and correlation. The latter subject, too, as paleontology becomes more complicated, requires more expert knowledge and background. Only the paleontologist can cope with the intricacies of correlation. These must be based on accurate fossil determinations, which in turn involve morphology and the legalisms of nomenclature.

The difficulties of dating by fossils and correlation, especially the time required for accurate paleontological work, lend impetus to the search for other methods of [dating and] correlation. Some of these have proved useful and faithful in restricted areas. The day may arrive when strata can be dated in years with reasonable accuracy by chemical or radioactive means. Then Paleontology will have lost the little practical value it now has and will become the exclusive concern of paleontologists.

We have just looked into the factors contributing to a slowing down of interest in pure paleontology. Now let us look at the future of paleontology in the United States, to see whether or not it will be worth while for an eager youngster to elect it as a career in the face of the present waning interest.

Although thousands of species and genera are now known, it is my belief, based on years of collecting in all parts of this country, that we have much descriptive work ahead of us. In my 32 years of collecting I have accumulated many new or little known fossils and know that we have barely begun in our work of description. The acidizing program carried on at the National Museum since 1935 is an illustration. More than 50 tons of limestone [of all ages above the Pre-Cambrian] have been dissolved to produce an enormous harvest of new species and genera.[22] This vast land of ours has many treasures still to be found and the descriptive phase of our science has many years to run.

Poor coverage of fossils in many parts of the geological column is another expression of this necessity. I am engaged in a study of the Permian brachiopods of the Glass Mountains. To help me in the identification of my specimens only two [extensive] monographic treatments of North American Permian brachiopods have ever been prepared.[23] For Pennsylvanian brachiopods we have a single monograph.[24] The same is true for the Mississippian. If one examines the brachiopod ascent through the Paleozoic an interesting diminution of many families takes place in the Mississippian and Pennsylvanian. I attribute this not to freak conditions in these periods, but to lack of paleontological work in the macro-faunas.[25] It is possible to go on endlessly in this vein with all groups of animals and periods, but it would not make the point clearer.

Time will not permit an extensive dis-

cussion of our enormous need for more morphological studies. A great number of our fossils still lock secrets in their interiors. Classification must await the unlocking of these doors to morphology. This is especially true of hosts of types that need sectioning and dissection before classification can progress. Curators in charge of types in the future must adopt liberal views in this regard. Application of statistical methods will also help to stabilize many of our species, especially among generalized types.[26]

Another need in the future is for family or ordinal revisions based on extensive collections that will take blocks of related species and genera and subject them to close scrutiny. Such studies are the best way to understand the relationships of many of our fossils. This will permit revision of species of a genus and genera of a family. Such studies sharpen generic conceptions and make it possible to propose new genera or make synonyms with greater assurance of accuracy and permanency and with a better perspective as to relationships.[27]

Modern correlation is not on a sound basis because the faunas of so few of our formations have been described or studied and our methods are not good.[28] It is a common practice at the present time, for example, to use single types of fossils for correlation. I am guilty of this practice, too, but have warned my reader[29] that my conclusions can only be regarded as tentative. The Upper Paleozoic is zoned on the basis of fusulines, but some of the correlations do not agree with those based on other groups such as the brachiopods or the goniatites. It is my view that we cannot have accuracy in correlation until the bulk of each fauna is known [for any given formation]. This means a vast amount of future work. This could, of course, be obviated if we all agreed to accept age assignments and correlations based on one group alone. This convenient course, however, will not lead us to the truth. We must, therefore, learn about the faunas, their movements in time and space and their variations from place to place. In addition to broader methods of correlation, reexamination of guide fossils is needed.[30] Close check must be made on specific identifications and all ranges, horizontal and vertical.

Parts of the United States have never had paleontological study. I point to the Appalachians from New York south, especially the southern parts where a vast Paleozoic sequence of 30–40 thousand feet is known. In general, the Paleontology applied to this extensive region is that of James Hall and the New York Geological Survey,[31] as evidenced by the large number of New York species recorded in the cursory work. The southern Appalachians includes many hundreds of feet of rock totally different in facies to supposed contemporaneous strata in the Northwest and Midwest and containing fossils which cannot be properly identified with New York species.[32] The same may be said for our West where most of the Paleozoic strata are actually still unknown paleontologically.[33] Alaska is another region which is virtually a paleontological blank.[34] In these vast areas the stratigrapher has multiplied formation names many times over, but the paleontology is still to be done.

In paleoecology a vast amount still remains to be done, but much of it actually will require the skills of the physical chemist and physicist rather than those of the paleontologist. The latter can, however, work out the relationships of species to one another, a phase of modern ecology of considerable interest. A study of this facet will not be easy, but closer observation of fossil occurrences together with local faunal studies should reveal interesting relationships.

In summarizing future work to be done [in pure paleontology], I can say with assurance that we have barely begun in our descriptive work, that morphology still offers an open field, that family and ordinal revisions based on first rate collections are needed to solidify our classifications, that the principles and practices of correlation and the use of guide fossils need restudy, that many parts of the United States have never been carefully collected[35] and much effort is still needed in paleoecology, especially relationships of the fossils to each other. Paleontology is thus a great field still in the qualitative stage with basic work for several generations.

It should be obvious to any of you who agree with me that the waning interest in Paleontology is a serious problem. No ready or simple solution exists to the various trends dangerous to unfettered paleontology.

Nevertheless, the problem can be attacked on several fronts. Each inimical trend mentioned earlier can be nullified, all or in part.

1) The general low popularity of Geology and its various branches including paleontology has been a concern of our leaders for some years. The American Geological Institute is a direct outgrowth of this apprehension. The program of popularizing geology to the public will take many years of constant selling before success will be attained. I think the best attack is on the youth of the country. It is, therefore, incumbent on everyone of us to encourage youngsters and intelligent amateurs who may have a geological bent.

Geology and paleontology have a high hobby and cultural value. They are ideal subjects for the high school, where they could be taught as a prescribed science to give young people a better conception of the world they live in. Any of you in a position to do so should agitate for adoption of geology in the high school. I had my first geology in a New York City school from a very inspiring teacher.[36]

2) We cannot curtail the scope of Paleontology in any way. Even though now very complex, the subject is bound to become more and more complicated. In teaching, however, classification can be taught on a family and ordinal basis rather than a genus and species basis as now. This will have advantages in fitting broader relationships into the student's mind. We should also encourage the making of catalogues of genera and species without attempting harmful subjective synonymies, better to summarize and organize our knowledge.[37]

3) Teaching of Paleontology must emphasize the zoological and biological sides of the subject rather than the stratigraphical. Micro-organisms should be treated in their proper places in the animal and vegetable kingdoms rather than as a separate science. Stratigraphy must be a requisite to Paleontology because the vertical distribution of fossils is information vital to an understanding of them; but the stress must be on fossils, their morphology, taxonomy, evolution and paleobiology, if we are to revitalize the subject.

4) The several branches of Paleontology should be reunited in the common cause of better Paleontology. Study of evolution, paleoecology, distribution and correlation are subjects of kindred interest to all paleontologists, vertebrate, invertebrate, micro and plant. These four groups fell out because of the complexities of their subjects and the disinterest of each group in the subject matter of the other. However, all of them can profitably unite on the common ground of principles applicable to all branches of paleontology.

5) Inasmuch as physical stratigraphy and paleontology are [so intimately involved with each other and] so complicated and will in the future become even more so, I suggest that lithostratigraphers and paleontologists be teamed in stratigraphic problems.[38] In this way the best effort of each can be brought to bear on a study. It will also leave each one of the team freer to further his own research. I suggest, too, that more pure paleontology be encouraged in organizations supporting paleontologists.[39]

6, 7) Standards in preparation of fossils and paleontological papers should be improved. Our modern mechanical facilities are so good that almost all fossils can be prepared for interior details in reasonable time. Our photographic equipment and films are superb and no excuse is apparent for poor illustrations. Therefore, I think universities should create courses in preparation of fossils, preparation of illustrations, paleontological methods and drawing and preparation of papers that would help to make practices more adequate and more uniform.

The paleontologists as a group should work for simplification of the International Code of Nomenclature and a return to the principle of priority and self-reliance rather than to a lengthy and costly resort to plenary power.

8) Our economic conditions call for a reorientation of values. The young man or woman who wants to make a career of pure paleontology will have to decide which is more important: his career or his standard of living. Salaries in paleontology will probably always lag behind those of more practical sciences, but will nevertheless be adequate for the family that is moderate in all its goals. Thus a career dedicated to paleontology will always be possible but may be somewhat Spartan.

If interest in paleontology is waning, as I say, and economic conditions for paleon-

tologists are not likely to brighten much in the future, what inducement will entice capable people into the field? The incompleteness of our knowledge, organization of what we now know, and the vast amount still to be done are the real inducements. Great opportunities to make an impression on our science are available to all men of ability; the opportunity to become a real authority with influence on the science is there for all who will work for it. The challenge of new facts to be found, new taxonomic arrangements to be made and organization of our facts, all in a science still in early youth, is the great appeal of Paleontology.

In conclusion I want to say that I believe paleontology [synonymous with paleobiology] is an independent science with the primary aim of making known the kinds of ancient animals and plants, their anatomy, biology and evolutionary descent. Paleontology is not biology nor is it geology; it is a science combining all of one and part of the other. Paleontology is not the handmaiden of stratigraphy, but is an independent science to which stratigraphy contributes the order of sequence of events. Stratigraphers[10] may use fossils for their own designs as they do mineral grains to help them identify rocks, but correlation, because of its morphological intricacy and need of accuracy, should be left to the paleontologist.

Paleontology is a very important study because it is only through continued collecting and description of fossils that the evolutional pattern of life will be understood. Biology shows the mechanics of evolution, but the pattern can only be learned through fossils. If man is to know the past and, perhaps, see the trends of the future through the patterns of evolution, he must assiduously study fossils.

To the young men, I say, that if you see the dangers mentioned as I do, work hard for changes that will bring paleontology to an honored place among the sciences. The paleontology of the future will require an imaginative and devoted group to revivify it and to raise its standards. Any change for the better must come from you. This is a challenge well worth your best effort.

FOOTNOTES

[1] The present discussion is concerned almost wholly with Invertebrate Paleontology because the fossil plants and vertebrate animals have not been so widely used in stratigraphy as the invertebrates. The Paleobotanists and the Vertebrate Paleontologists are quite self-sufficient. The former group has allied themselves with the Botanical Society, whereas the Vertebrate Paleontologists have their own organization which meets separately from the Paleontological Society. Both of these organizations are closely allied with the biological sciences and have not yet been faced by some of the problems raised here.

[2] In studying the most recent list of the Paleontological Society some interesting facts may be gleaned. Based on United States citizens only, the Paleontological Society has a few more than 100 members who can be classed unequivocally as paleontologists. This number includes the few paleobotanists and vertebrate paleontologists in the Society. The Society has about 81 unquestionable invertebrate paleontologists.

[3] By experts I mean men who have fairly well mastered entire groups. Actually, no paleontologist in this country is expert in pelecypods, or gastropods throughout the ages, nor has anyone mastered all of the cephalopods. Few paleontologists have mastered one or more groups in an era, although some are quite expert in one or more groups for one period. Some of the experts mentioned above are actually skilled only in small or restricted groups.

[4] Most of the experts in Arthropoda are skilled in small groups only.

[5] The United States has never had many workers in graptolites. It is comforting to know that some young men are interested in some of the groups not now occupied, but it is too early to say whether or not their interests will be along biological or stratigraphical lines.

[6] See brochure on "The importance and needs of systematics in biology" sponsored by the Division of Biology and Agriculture and organized by the Society of Systematic Zoology, National Academy of Sciences, National Research Council, Washington, D. C., April 22, 1953, Appendix A, p. 1–9.

[7] See Geotimes: Our responsibility: v. 2, no. 6, Dec. 1957, p. 5; Is geology asleep at the switch?: v. 2, no. 8, 1958, p. 5.

[8] See Interim Proc. Geol. Soc. America, 1958, p. 2 (only five papers in paleontology at the Atlantic City session), March 1958.

[9] Any moment in any geological period can be compared to the present day. The world in the past was extremely complicated and was populated by thousands of animals and plants as it is now.

[10] Colleges economize on faculty by having the paleontologist teach stratigraphy or the stratigrapher teach paleontology. This is a better arrangement than not having either subject taught, but the result may lead to bias, which is seldom on the side of biological paleontology because the colleges having this arrangement usually are poorly provided with collections of fossils.

[11] The great urge to establish correlations with

a minimum of labor and materials from small samples of rock has led to the great interest in micro fossils. This is of considerable economic importance, but like all correlations based on insufficient information may prove wrong or misleading.

[12] This is the situation that obtained at the time the speech was given. Conditions now are somewhat better for the physicists, chemists and engineers in the government. The salary lag between physicists and geologists is described in Geological News Letter: v. 7, no. 8, Feb. 1956, p. 5.

[13] This differential still exists, but the Interior Department has petitioned the Civil Service Commission in behalf of the geologists.

[14] See KNIGHT, J. B., 1947, Paleontologists or geologists: Geol. Soc. America Bull., v. 58, p. 281–286; WELLER, J. MARVIN, 1947, Relations of the invertebrate paleontologist to geology: Jour. Paleontology, v. 21, p. 570–575; NEWELL, N. D., & COLBERT, E. H., 1948, Paleontologist—Biologist or Geologist?: *idem.*, v. 22, p. 264–267; NEWELL, N. D., 1954, Toward a more ample Invertebrate Paleontology: Bull. Mus. Comp, Zoology, Harvard Coll., v. 112, no. 3, p. 93–97.

[15] Paleontology, or rather Paleobiology, differs from Biology because it is dependent for its sequence on geology, and the enormous time factor involved introduces an element foreign to biology.

[16] The unit of correlation is the species, although some correlation by genera is possible. The identification of the species is dependent on correct solving of the genus to which the species belongs. Such careful identification is the responsibility of the paleontologist who must have ingenuity in exposing generic and specific characters. The day of identification by the exterior alone is long since gone.

[17] GRABAU, A. W., 1924, Principles of stratigraphy, 2nd ed.: A. G. Seiler, New York, p. 1.

[18] KRUMBEIN, W. C., & SLOSS, L. L., 1951, Stratigraphy and sedimentation: W. H. Freeman and Company, San Francisco, California, p. 4.

[19] *Idem*, p. 4.

[20] The Federal Survey and some state surveys maintain paleontologists to assist the field mapper. The same is true of a number of oil companies who have paleontologists primarily to identify or check stratigraphic horizons in wells and in the field.

[21] Here is where I trod on tender toes. One of my colleagues who is interested in both paleontology and stratigraphy said that he resented being "read out of the party." It is obvious that it would be best for paleontology to be done by a highly skilled scientist, but it is not possible to insist too strongly on the point. Some stratigraphers prefer to do their own paleontology and some of them do very creditably; it would, however, be better for them to concentrate wholly on paleontology and do a still better job. The same may be said for the paleontologist who tackles some phases of physical stratigraphy that are now highly technical and best done by one specialized in that work.

[22] The importance of creating new genera and species has been questioned in some quarters (WELLER, J. M., 1952, Analysis of trilobite generic nomenclature and its implications regarding progress in Paleontology: Jour. Paleontology, v. 26, no. 2, p. 137–147), and many stratigraphers lament bitterly over the magnification of names. Proliferation of genera and species will stop only when few genera or species are left to describe. The broad minded stratigrapher should welcome new genera and species as tools to better understanding and the progressive paleontologist will recognize them as additional blocks in the edifice of evolution.

[23] These two monographs are: GIRTY, G. H., 1909, The Guadalupian fauna: U. S. Geol. Survey Prof. Paper 58, and KING, R. E., 1930, The geology of the Glass Mountains, Texas. Faunal summary and correlation of the Permian formations with description of Brachiopoda: Univ. Texas Bull., no. 3042.

[24] This is DUNBAR, C. O., and CONDRA, G. E., 1932, Brachiopoda of the Pennsylvanian System in Nebraska: Nebraska Geol. Survey. This book covers far more territory than Nebraska and includes many Permian species (about 20 per cent).

[25] In this connection I submit the accompanying illustration (text-fig. 1) which shows a spindle diagram for the brachiopods based on the approximately 1600 known genera. The great reentrants in the Silurian, Mississippian and Pennsylvanian, in my opinion, are a reflection of the few brachiopod studies in these periods. The same is true for the deep indentations in the Triassic. The Tertiary and Recent indentations are, however, real; a definite decline in the brachiopods occurs after the Cretaceous.

It is interesting to point out that before the appearance of my "Chazyan and related Brachiopoda" with its numerous new genera combined with the work of Spjeldnaes, the maximum bulge of the brachiopods was in the Devonian.

[26] Statistical methods will help to sharpen our species, but it is doubtful that they will cut down the supply.

[27] The revision of the Orthoidea and Pentameroidea by Schuchert and Cooper (Mem. Peabody Mus. Nat. History, v. 4, pt. 1, 1932) is an example of the type of study that yields fruitful paleontological results. This is a monographic treatment of two homogeneous groups of brachiopods and emphasizes their morphology and relationships. The study was based on the best collections in the United States and included specimens of nearly all the genera known in these groups at that time. Relationships between genera and groups of genera were clearer in this study than one dealing with heterogeneous groups of brachiopods found together in one or more formations.

[28] A study of the Lexicon of geological names will make it clear that we have a long way to go in correlation. This is also made clear in the charts sponsored by the National Science Foundation and published by the Geological Society of America. A great deal of modern correlation consists of assertions of relationship rather than proof. Actually proving a correlation is difficult, but the aim should be like that in a legal trial, to

demonstrate the correlation "beyond reasonable doubt."

[29] The correlation of the Ordovician formations in the "Chazyan and related Brachiopoda" (Smithsonian Misc. Colls., v. 127, pts. 1, 2, 1956) was based wholly on brachiopods. It was clearly stated that the scheme can only be regarded as tentative until more extensive collecting and description of other groups brings the whole into better focus (p. 6,7).

[30] The true range of fossils will really never be known until the last specimen is collected. However, approximately 150 years of collecting have given sufficient experience to be reasonably sure that some species are in reality good guide fossils. However, many of our species are so rare or scattered that it will take many more years of collecting to establish their true range. The more extensive the collecting, the greater the range of many species and genera is extended, but only by this intensive collecting can the true range be determined.

[31] These remarks are not intended to belittle the paleontology of James Hall; they are designed to emphasize the fact that much of the Paleontology of New York, especially the Devonian, is in need of revision. It is these unrevised names that have been so extensively used in the Appalachians and many of these New York names have been carried southwest beyond their facies and their usefulness.

[32] Unrevised New York names have been extensively applied in the Ordovician, Silurian and more especially in the Devonian.

[33] Few monographic studies have ever been prepared on the Paleozoic fossils of the Rocky Mountains and west. Walcott's fossils of the Eureka District of Nevada is one of the best known works. The fossils of the upper Paleozoic of the West are actually only slightly known.

[34] Alaskan Paleozoic fossils have generally only been listed, not monographed. Many of the published lists consist of misidentified species, specimens identified to the nearest known form in the United States or Europe in the hope of establishing a correlation.

[35] Here I make a plea to all collectors and especially to University professors and instructors to conserve their fossils. Some species are common and the loss of them is not serious, but some localities are now nearly or completely exhausted. At many Pennsylvanian localities in Texas that I have visited it is no longer possible to obtain any of the larger species. These have been collected out. If we ever wish to apply statistical methods to our fossil associations, we may be hard pressed to find collections adequate for the study. Rare fossils should be turned in to their professors by students so that ultimately enough of them will be obtained for proper understanding of the species.

[36] The amateur must be encouraged. Rather than deride his efforts or obstruct him, it is well to help him and teach him to conserve his good specimens and induce him to place his collection in a permanent and safe place when he is through with it.

[37] The most useful catalogues are those recording the original name of the species and not attempting synonymy or selecting types. It is true that a type is fixed when a type species is designated and it makes little difference for its permanence whether it is intelligently fixed or not. It is best, however, to leave fixing of types to the monographer of the genus or species who is better able to judge the quality of the specimen and species available for type within the limits imposed by each case.

[38] My work on the Ordovician of the Shenandoah Valley with Dr. Byron N. Cooper is a good example of the sort of cooperation I have in mind. B. N. Cooper measured most of the sections and worked out lithological details; G. A. Cooper collected the fossils and worked out the correlations. Naturally, each checked on the other and the result was better understanding by both workers. COOPER, B. N., & COOPER, G. A., 1946, Lower Middle Ordovician stratigraphy of the Shenandoah Valley, Virginia: Geol. Soc. America Bull., v. 28, p. 35–114.

[39] Some oil companies are starting attractive research positions, especially in paleoecology. The difficulty of obtaining good libraries and extensive collections may limit effective work on fossils.

[40] For their work in the field stratigraphers do not need the elaborate naming of fossils used by the paleontologist. They can rely on any physical character as long as it is persistent and widespread. However, for correlation identification must be exact; exactness calls for throughness and care in identification. Fossils can thus be useful to a stratigrapher in field work and the multiplicity of names should be no real problem to him.

[41] The situation as outlined above has been a burning problem for many years. I quote a paragraph from a letter written by Dr. Charles Schuchert of Yale University to Dr. Frank Springer:

"If you are aware of what these places have been doing for the past ten years, you will see that no one in pure paleontology has been turned out. This is in particular true for invertebrate paleontologists, and while a number of young men have been developed, most of these men are really geologists, that is, stratigraphic paleontologists like myself. It seems to me that this state of affairs here in America is somewhat alarming and I am doing all I can to break down the extraordinary dominance of the geologists who are not trained in paleontology and particularly those not caring a rap for paleontology as a guide in their stratigraphic work. If this state of affairs goes on for ten or fifteen years longer, the older men will have gone and there will be no crop of new men to take their places. Jackson was forced out of Harvard and I think Eastman is going so that at present there are in the universities no paleontologists working in pure paleontology."

The fact that Professor Schuchert recognized in 1911 a situation similar to the one I outline may indicate that Paleontology is a durable subject and that its few practitioners are difficult to discourage. Perhaps we can look forward to a golden age if we solve some of the problems outlined.

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PALEONTOLOGICAL NOTES

ON THE VALIDITY OF *SCHWAGERINA* AND *PSEUDOSCHWAGERINA*

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Among the most useful fossils for zonation and correlation of early Permian rocks are the fusuline genera *Schwagerina* and *Pseudoschwagerina*. Both are widely distributed and morphologically distinctive, but, unfortunately, the names have been the subject of much confusion. The problem was legally settled in 1954 by Opinion 213 of the International Commission on Zoological Nomenclature which fixes the generotype of *Schwagerina* as *Borelis princeps* Ehrenberg, 1842, [not *Schwagerina princeps* Möller, 1878 = *S. moelleri* Rauser-Chernoussova, 1936] and that of *Pseudoschwagerina* as *Schwagerina uddeni* Beede & Kniker, 1924.

A protest was recently made, however, by my esteemed colleague, Madam Rauser-Chernoussova, in a paper entitled, "On the impossibility of recognizing *Borelis princeps* Ehrenberg, 1854 as the typical form of the genus *Schwagerina* Moeller, 1877" [in Russian]. This title exactly contradicts the words of Möller in his original definition of the genus which read "Als eine typische Form derselben sehe ich die *Schwagerina princeps* Ehrenb. an.[6]" (The footnote refers to plate XXXVII, X, C, figs. 1–4 of Ehrenberg's paper of 1854.) Nevertheless, Madam Rauser-Chernoussova argues that this cannot be regarded as the type because (1) there is no evidence that Möller had actually studied Ehrenberg's material, and (2) Ehrenberg's specimens are not suitable as types because (a) their exact locality was not given, and (b) they are poorly preserved. She regards the type of *Schwagerina* to be a form from China which Möller in 1878 misidentified as *S. princeps* and which she, in 1936 renamed as *S. moelleri*.

Although the decision of the International Commission (Opinion 213) is probably irrevocable, even if desirable, a review of the problem may help to avoid further confusion. This seems the more necessary since, as it seems to me, Madam Rauser-Chernoussova has in some important respects misinterpreted the evidence in the case.

Before 1877 all recognized fusulines were referred to the single genus *Fusulina* Fisher de Waldheim, 1829. In that year, however, Möller began his epoch-making studies of the fusulines by proposing three additional genera, *Schwagerina*, *Fusulinella*, and *Hemifusulina*. The last two were based on characters of the wall and septa, but *Schwagerina* was distinguished only by shape, and was proposed to include globular and thickly fusiform species. The original description (in full) may be translated as follows:

> *Schwagerina* n.g. Shell round or inflated in the middle and, as in the foregoing genus [*Fusulina*], spirally enrolled, divided internally by septa into chambers, and of porous structure. The somewhat numerous septa consisting of a single, rather thick lamella, are simple and without folding except in the neighborhood of the axis, where there is a local, sometimes very strong and regular folding which gives rise to a real and marked septal net. The septa as seen in cross section join the shell at a right, or somewhat acute angle. The septa possess a median opening [tunnel] as in true *Fusulina*, through which all chambers remain in complete communication with each other. The first chamber is barrel shaped or elliptical. The surface is marked by elliptical, meridional furrows which, as in *Fusulina*, correspond to the septa. In fully grown shells the aperture is closed by the gradual decrease in the height of the last whorl.
>
> This genus I permit myself to name in honor of Mr. C. Schwager whom, as I believe, we have to thank for the first fundamental investigation of the so-called globular fusulines. I regard *Schwagerina princeps* of Ehrenberg as a typical form though that species has been unjustifiably united by certain paleontologists with *Fusulina robusta*. The form described under that name by Meek appears identical with the Russian form, yet this union of the two forms is opposed by the folding of the septa indicated (if correct) in Meek's pictures of the American form.
>
> In addition belong here the abundant little species so common in the Carboniferous limestones of Russia, *Schwagerina sphaeroidea* Ehrenb. (= *Borelis sphaeroidea*,[9] *B. constricta*,[10] *B. labyrinthiformis*,[11] and *B. palacophycus*[12] Ehrenb.) and *Schwagerina Hoeferi* Stache. In the illustrations given by Ritter and Hauer the meridional furrows should be added to the partly preserved shells.

No illustrations accompanied this discus-

sion and no other species were mentioned. Although Möller's words, "Als eine typische Form derselben sehe ich die *Borelis princeps* an" may not constitute a clear and unequivocal designation of the type species of the genus *Schwagerina*, the generic discussion is built around that form, and the small species named in the last paragraph were merely mentioned in passing, and all of these were later included by other workers in the genus *Staffella*. Furthermore, later workers have invariably cited *Borelis princeps* Ehrenberg as the genotype (e.g., Schellwien, 1898, p. 257).

The basis for confusion arose in 1878 when Möller continued his study of fusulines and introduced illustrations of thin sections of shells collected by von Richthofen near Shanghai, China which he (Möller) misidentified as *Schwagerina princeps* (Ehrenberg). These sections reveal a tightly coiled juvenarium followed by rapid inflation to high adult whorls in which the septa are only gently folded. In the absence of sections of Ehrenberg's types these characters were subsequently accepted as the significant characteristics of the genus *Schwagerina*.

Ehrenberg's types of *Borelis princeps* meanwhile had been preserved in the museum of the Geological-Paleontological Institute at the University of Berlin and in 1935 were loaned by Dr. Otto Schindewolf to Dunbar and Skinner for critical study with permission to cut thin sections. The sections revealed that the volutions expand gradually, that chomata are lacking, and that the septa are intensely folded throughout so that the species has exactly the characters for which Dunbar and Skinner had erected the genus *Pseudofusulina*.

Faced with this dilemma, Dunbar wrote to Dr. Stiles, who was then Secretary of the International Commission on Zoological Nomenclature, asking advice as to whether the named genotype (*Borelis princeps* Ehrenberg), or the specimens from China, later figured by Möller, should be accepted as the types of *Schwagerina*. Unfortunately, Dr. Stiles was in his final illness and the Commission was essentially defunct. The reply to Dunbar's letter came nine years later, from Dr. Hemming who had become Secretary of the revived Commission. One can only wish that the Commission had used its plenary power in 1935 to validate the species figured by Möller in 1878 (= *Schwagerina mölleri* Rauser-Chernoussova, 1936) instead of the named genotype (*Borelis princeps* Ehrenberg). Lacking action by the Commission, however, Dunbar and Skinner felt obliged to follow literally the International Rules (e.g., Opinion 14) and accept the named generotype. This principle has subsequently been covered by Opinions 169, 173, 175, 179, 181, and 188 in which the decision has invariably been to accept the named generotype instead of misidentified specimens that may have been studied by the author of a new genus. There seems, therefore, to be no escape from the conclusion that the generotype of *Schwagerina* is the species from Pinega Valley, Archangel, described by Ehrenberg as *Borelis princeps* in 1842 and 1854.

While it is unfortunate that the exact locality of his types was not recorded by Ehrenberg, this is not sufficient to invalidate the species; many of the older species have the same shortcoming and not a few (e.g., the types of *Halysites*) are from glacial drift so that their original localities can never be recovered. In the case of *Borelis princeps*, moreover, the type material is preserved and numerous specimens have been sectioned and described so that the specific characters are well known (Dunbar & Skinner, 1936).

Madam Rauser-Chernoussova has misinterpreted our work, however, in thinking that the Ehrenberg material is so poorly preserved as to leave the shell characters in doubt. To be sure, the shells and matrix are both completely silicified and the preservation leaves much to be desired so that our illustrations are not as good as we would wish. However, the walls are thick, as in the Schwagerinidae (much thicker than in the Fusulinellidae), and in places they show unmistakable evidence of alveolar structure. The sections also show clearly that chomata are lacking and that the septa are strongly and regularly folded. Some of the axial sections also show clearly that the height of the volutions increases slowly and gradually from the proloculus to the final whorl. The statement quoted, out of context, by Rauser-Chernoussova that the early whorls "are altered to clear quartz and do not show

plainly" (D. & S., p. 86) referred to one axial section (pl. 10, fig. 8); on the contrary, two of the sagittal sections figured (figs. 10 and 11) show all the inner volutions. Having just restudied the negatives made of this material in 1936, I feel sure that all the essential generic characters are shown by Ehrenberg's material and that *Borelis princeps* is a rather small species similar in shell morphology to *Schwagerina bellula* Dunbar & Skinner of the American Lower Permian and *S. uralica* Krotow of the Lower Permian in the U.S.S.R.

Whereas it is possible that Möller had sectioned and studied the Chinese shells in 1877, there is no evidence whatever that he had done so. If his study of the fusulines had been interrupted (by death or otherwise) before 1878, the genus could only have been interpreted in the light of Ehrenberg's types of *Borelis princeps*. Although these had not been sectioned in 1877 and may not actually have been seen by Möller, their characters are now known through the publication of Dunbar & Skinner and the types are still available for study.

The confusion introduced by Möller's misidentification of the shells collected by von Richthofen is most unfortunate but is easy to condone in view of the pioneer nature of his study. It is true that during the sixty-eight years between 1878 and 1936 the genus *Schwagerina* was interpreted in the light of the Chinese species, *S. princeps* Möller, 1878 (not *S. princeps* Ehrenberg, 1854 = *S. moelleri* Rauser-Chernoussova, 1936). But in the much more extensive literature written since 1936 in America, Japan, China, and Austria the genus has been interpreted in the light of the named generotype, *S. princeps* Ehrenberg, whereby *Pseudofusulina* Dunbar & Skinner becomes a synonym of *Schwagerina* Ehrenberg, 1877 and *Schwagerina* of authors, 1878 to 1936, becomes *Pseudoschwagerina*. Since the latter interpretation has been validated by the International Commission on Zoological Nomenclature its adoption appears to be the only hope of avoiding perpetuation of the unhappy confusion.

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THE INTERNAL STRUCTURE OF *DIPLOGRAPTUS PEOSTA* HALL

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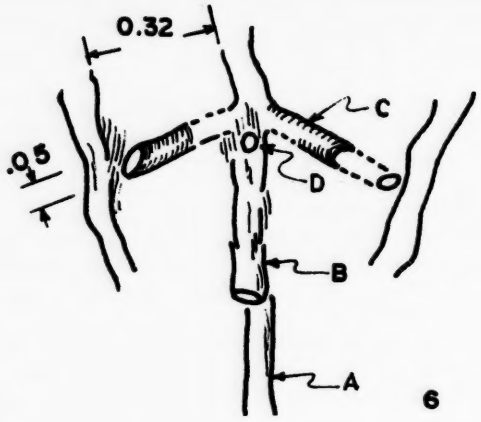
INTRODUCTION

There have been many studies of the Diplograptidae (among others, Wiman, 1893; Ruedemann, 1895; Törnquist, 1897, cf. Bulman, 1955, V95–V98). However, little has been discovered to this time about the detailed internal structure of *Diplograptus*. Present knowledge appears to be confined to a view of the "median septum" and the "common canal" in longitudinal section (cf. Moore, Lalicker, & Fisher, 1952, p. 724, fig. 22—6). This, of course, is due to the fact that two-dimensional carbon films of entire or partial rhabdosomes are most often preserved, or, at any rate, recovered. Three-dimensional preservation is a rarity.

Bulman's informative treatment of the class Graptolithina and order Graptoloidea (1955, V43–V94) may be taken as summarizing extant knowledge. Under the generic description of *Diplograptus* McCoy 1859 (p. V85) or in the illustrations of this genus (fig. 63) or the illustrations of diplograptid type of development (fig. 41), the structures to be described here are not indicated.

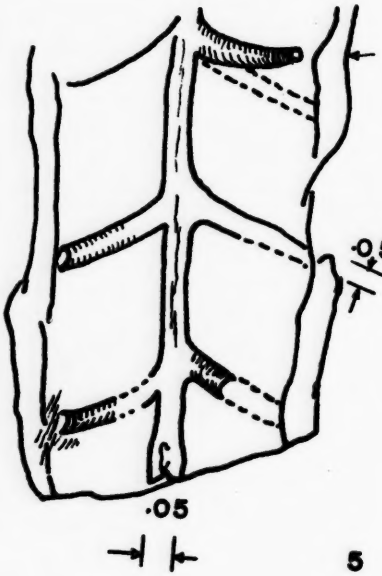
2 A



6

3 A

2 B



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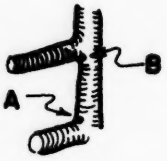
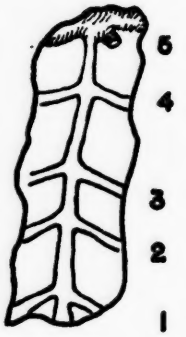


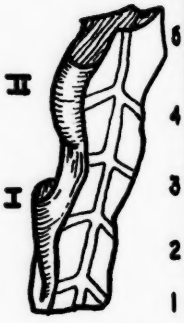
2 D

1

2 C



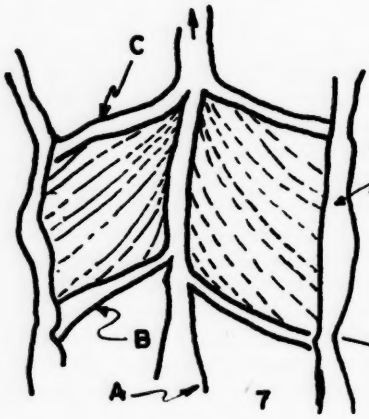
3 C



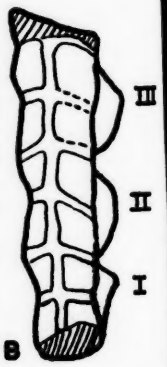
3 B

4 A

4 C



7



4 B

While measuring three-dimensional fragments of *D. peosta* (text-fig. 1) obtained from the basal Maquoketa shale of northeastern Iowa, as part of a larger ongoing study of the fauna and paleoecology of this zone, some natural unflattened half specimens were found. These came from Station 6.8 near the town of Volga, Clayton County, Iowa, and Station 8.4, Kaufman Street Quarry, Dubuque, Iowa. (Details of these and other sections are now in preparation and will be published separately.) Each of these half specimens had been separated at right angles to the central axis. Study of the median septum in plan-view was thus made possible.

The details given below and in the text-figures reveal a type of structure known in other of the diplograptids, for example, *Climacograptus sharenbergi* (Bulman, 1955, fig. 34.2 and text p. V51) but not previously recorded for the genus *Diplograptus*. Numerical data on internal structures are provided in Table 1.

INTERNAL STRUCTURE AND OTHER DATA

A series of camera lucida drawings (text-figs. 2a–c,3a–c,4a–c) were made and detailed measurements taken by using a micrometer eyepiece (100 divisions in 10 mm.). Photographs being quite inadequate for small details of this kind, following Bulman (1955), only inked-in camera lucida drawings were used for illustrations.

All figured specimens are from the same locality and horizon and are referred to by the box number on the micro-slide on which they are mounted. Table 1 summarizes the numerical and related data on the three specimens.

Apertural width.—Study of Table 1 indicates that the three half-specimens each from a different individual diplograptid have about the same length, width, and thickness. Apertural width increased by varying amounts as the colony grew, ranging from 0.15 mm. (spec. 33.1) to .03 mm. (spec. 45.1). The one specimen bearing three thecae indicates a constant increment in apertural width of 0.05 mm.

Distance between thecae.—The distance between thecae (measured between centers of two successive theca) is a variable quantity ranging from 0.3 mm. (spec. 33.1) to twice that amount, namely 0.6 to 0.7 mm. (spec. 34.1 and 45.1)(see text-fig. 2a). Whether the increment is in multiples of 0.30 mm. can be determined by a check of a few of the larger unsectioned specimens. When this is done at random (Spec. 1.1 and 25.1), a range of 0.6 to 0.7 mm. is obtained.

Numerical data on lateral lists and virgula.—Figures given in Table 1 are immediately convincing on the relatively constant distance between successive list-pairs. A list is a supporting tube connecting the virgula in the present examples to the rhabdosome (text-fig. 6). The constant distance for

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TEXT-FIGS. *1–7—Diplograptus peosta* Hall. All figures are inked-in camera lucida drawings. Dimensions shown are in millimeters and were measured with a micrometer eyepiece attached to a binocular microscope. Figures specimens are on deposit at the Department of Geology, University of Wichita. Closely-spaced lines and ovals represent sediment. Roman numerals denote successive theca, but do not correspond to ontogenetic stages. Other numbers (exclusive of indicated measurements) denote successive list-pairs. *1*, unsectioned fragment, ×17, Loc. 6.8, specimen 1.1. *2*, natural half section, Loc. 6.8, specimen 33.1; A, dashed line indicates distance between centers of two successive theca; this is one of the measurements given in Table 1; B, showing virgula and list branches in relation to the theca; C, median septum in plan view, one half side only is shown though visible on both sides of virgula, and the virgula-list system; D, points "A" and "B" indicate where measurement between successive list-pairs was made. *3*, natural half section, Loc. 6.8, specimen 45.1; A–C, same as 2A–C; note displacement of list-tube number 5, in 3C, *4*, natural half section, Loc. 6.8, specimen 34.1; A–C, same as 2A–C; compare placement of lists in relation to the theca, in figures 2B,3B, and 4B. *5,6,7*, detail of virgula and list-system. *5*, successive list-branches of virgula, arrow indicates displacement of list-tube from its groove; note thickness of virgula and list are the same; loc. 6.8, specimen 45.1. *6*, dimensions and actual state of preservation of virgula and one list-pair, A—central groove, B—virgula tube, C—list-tube, D—opening to portion of virgula tube; compare width of list-tube with distance between successive list-tubes shown in fig. 7; Loc. 6.8, specimen 33.1. *7*, median septum in plan-view, A—central grooves, B–C—list grooves, D—lateral wall; 12–14 distinct bands were counted in the median septum in a distance of 0.30 mm.; Loc. 6.8, specimen 33.1.

TABLE 1.—MEASUREMENTS OF INTERNAL STRUCTURES (IN MM.) AND RELATED DATA FOR *Diplograptus peosta* (HALF-SPECIMENS), BASAL MAQUOKETA OF IOWA, STATION 6.8

Specimen Number	Length	Width	Thickness	Number of thecae	Apertural width	Distance between successive theca*	Distance between successive list-pairs†	Length of protheca	Thickness of virgula	Thickness of lists	Length of lists
34.1	1.95	0.75	0.42	3	III—0.40 II—0.35 I—0.30	III-II—0.65 II-I —0.57 I‡—0.25	−0.30 −0.32 −0.27 −0.27 −0.27 −0.25	−0.25	.05	0.037	0.30
45.1	1.80	0.75	0.55	2	II—0.50 I—0.47	II-I —0.75 I‡—0.45	−0.35 −0.37 −0.27 −0.32	−0.17	.05	0.05	0.27
33.1	1.80	0.90	0.57	2	II—0.70 I—0.55	II-I —0.35 I‡—0.37	−0.35 −0.37 −0.30	−0.25	.05	0.05	0.32

* To be read as follows: between theca II and III, the distance is 0.65 mm. The distance is measured from the center of one theca to the next preceding. Roman numerals do not represent the actual position (i.e., ontogenetic development). Theca III, for example, merely denotes the third theca represented on the fragment where the count of theca began at the narrower end.

† A distance of 0.33 mm. between list-pairs 3 and 4 on specimen 3.1 (Sta. 8.4) was determined despite poor preservation of other list-pairs.

‡ This figure is the length of the metatheca.

thirteen list-pairs is $0.30 \pm .05$ mm. (see text-fig. 2d). This attests to the regularity of the process by which they developed. It should be kept in mind that three distinct individuals are represented, meaning three different biological entities each of which had to secrete a fine chitinous tube at a constant distance apart from its predecessors. One can postulate that an equivalent figure would be found in larger and other samples of this same genus and species.

The length of the lateral lists is also a constant of 0.3 mm. and equivalent to the constant distance apart of any two successive lists. For the thickness (diameter) of the chitinous tubes (lists) the figure $0.05 \pm .01$ mm. is indicated. Still another constant is the thickness of the virgula in the three specimens studied, i.e., 0.05 mm.

One can readily and logically extrapolate to the complete graptolite from such constants, because the specimens studied are not at the same growth stage. This is evidenced by the apertural width variation from one specimen to another. In other words, the constants would hold for various sectors of the same rhabdosome, since, in effect, our three specimens may be viewed as three such sectors.

The nearly identical thicknesses (diameters) of virgula and lateral lists also makes clear that the same process by which the central chitinous tube was laid down required little modification to give rise to lateral branches (lists) to act as supports or struts for the growing colony.

These lists meet the virgula at acute angles en-echelon fashion although the grooves are curved. Text-figure 5 shows an enlarged camera lucida drawing of a chitinous tube (list) displaced from the lateral groove in the median septum.

When first discovered, the observed virgula-branching list system was thought to be a possible variant of the stolonal system. However, as text-figures 2b,3b, and 4b show, when theca and internal structure were simultaneously brought into view, a list merged with the lateral wall at about midway down from the aperture of a given theca and the next preceding list's position corresponded to the prothecal region. They were thus obviously not related as are true stolons to the budding of thecae.

The virgula diameter did not vary along its entire course. It was possible to determine this even though whole sections were absent by erosion. This followed, because at either end, and also at some near midpoint, unflattened remnants of the chitinous tube remained (text-fig. 6).

In Table 1 the listing of measurements for distance between successive lateral pairs requires additional clarification. Measuring this distance between centers of two successive apertures included from top to

bottom, a metatheca and a protheca. Hence, for specimen 34.1, the distance between theca III and II, 0.65 mm., covers both the length of metatheca III and the length of the protheca (for definition of these terms, see Bulman, 1955, fig. 30, p. V46). It will be seen that this figure is close to the sum of the distances for two successive lateral list-pairs (i.e., 0.30+0.32=0.62 mm.) Similarly, the figure for distance between theca II and I corresponds closely to the sum of the respective list-pair distances. The last figure I* denotes the actual length of the metatheca which again corresponds to one list-pair's distance apart. The remaining list-pair distance is equivalent to the length of the protheca.

Variations in such close agreement can be seen for specimens 45.1 and 33.1 in Table 1. One can ask what does this close relationship denote? Study of text-figures 2,3, and 4 will make clear that list-pairs were deposited as supportive structures required by new thecal growth. Thus, the increment of length added by thecal growth would, in a sense, determine spatial placement of lists in the median septum. The close agreement in the figures between list-pair distances apart and thecal distances apart is thus a corollary of the interrelationship in which thecal growth seems to have triggered the mechanism for secretion of the chitinous lateral tube extensions of the virgula.

Median septum.—Bulman (1955, V52) pointed out that "information concerning its (i.e., the median septum) structure is lacking." It seems worthwhile, therefore, to record the observations made from the three half specimens (Sta. 6.8) and the six badly eroded half specimens (Sta. 8.4) in which portions of the median septum are nevertheless preserved.

The structure of the median septum appears as follows: in a distance of 0.30 mm. (i.e., the distance between two successive list-pairs), the writer counted ten to fourteen distinct bands. These are arranged enechelon fashion on either side of the virgula. The two curved limbs of the echelon are separated by a central groove in which the tubular virgula is imbedded.

All septum bands trend towards the angle formed by the younger of any two lateral lists and the central groove. The bands are wider near the older of any two successive lateral lists (see text-fig. 7). The tubular virgula and its list branches appear to be set in pre-existing channels within the median septum.

ACKNOWLEDGMENTS

Research for this paper was made possible by two National Science Foundation Grants (G-764, G-2933). Illustrations were financed by a University of Wichita Research Fund Award.

ADDENDUM

Since writing this paper I have had a chance to study the work of Paul Kraft (1925, Ontogenetische Entwicklung und Biologie von *Diplograptus* und *Monograptus:* Berlin, Palaeont. Zeit., Bd. VII p. 207–247, pls. V–XVII). The virgula is shown in longitudinal view (pl. XIII, and in greater detail in pl. XIV, fig. 6). Given the magnification it was possible to determine the thickness of the virgula in *Diplograptus gracilis* Roemer. That figure was found to be 0.027 mm. Kraft's excellent paper on the ontogeny of *Diplograptus* provides no information on the plan-view of the median septum, or virgula and list-branches.

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THREE DIMENSIONAL GRAPTOLITES IN THE MAQUOKETA SHALE (UPPER ORDOVICIAN) OF MISSOURI

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For several years we have been using samples of Maquoketa shale (upper Ordovician) of Missouri for the study of ostracodes and conodonts, in our micropaleontology laboratory. The samples used in the laboratory work are from Castlewood, Missouri, 18 miles southwest of St. Louis, a locality easily accessible to Washington University.

At Castlewood the Maquoketa is a shale from 15 to 20 feet thick, dark gray to greenish gray in color. At the base and near the top of the formation are several thin phosphatic conglomeratic zones. In places the zones are pyritized.

Approximately two feet from the top of the Maquoketa a weathered, light brown conglomeratic shale is present locally and this is used for our laboratory work. This material contains a very interesting and varied fauna; ostracodes, bryazoans, brachiopods, conodonts, pelecypods, and quantities of pieces of unpressed and apparently completely replaced graptolites. The unusual preservation and relative abundance of these graptolites seem to make it worthwhile to specifically note the locality.

The location: St. Louis County, in the S½ SW¼ sec. 15, T. 44N., R. 4., in the cut of the St. Louis and San Francisco railroad at telegraph post −2220, near Castlewood, Missouri, on the N. side of the RR right of way. A brief description of the section at this locality is as follows:

MISSISSIPPIAN		
Burlington	limestone, light brown, massive, crinoidal	50′
Fern Glen	limestone, gray, greenish-gray, buff, some red members, dense	18–20′
Bushberg	sandstone, brown to yellow-brown	6–10′
ORDOVICIAN		
Maquoketa		
	conglomerate, black pebbles in yellow brown sandy matrix, contains Bushberg fish teeth and some Maquoketa fossils, transitional	2– 6″
	shale, gray, soft, weathered, laminated, *Lingula* and fragments of *Diplograptus*	6–10″
	conglomerate, black pebbles in matrix of clay and sand, some pyrite, zones not continuous, rare unpressed graptolites, ostracodes, conodonts	2– 6″
	shale, reddish brown, weathers light brown, finely laminated, much pyrite, abundant unpressed graptolites, ostracodes, conodonts, bryozoans, etc.	4– 5″
	shale, gray, coarsely laminated (dark gray when wet, dries white gray), noncontinuous seams of pyrite, pieces of unreplaced *Diplograptus*, abundant *Lingula* in shale seams	15–18′
	conglomerate, black polished phosphatic pebbles in sandy clay matrix; possibly equivalent to the "depauperate zone" found in Iowa and Illinois	3– 6″
Kimmswick	limestone, exposed West end of cut	3– 4′

The fauna of this zone, with the exception of the conodonts, appears to be coated and replaced with a phosphatic material; the colors range from light to dark browns, and light to dark grays. Several samples were treated with dilute HCl and in many cases the graptolites, ostracodes and other elements of the fauna did not dissolve. A few of the graptolites which remained intact after being treated with HCL were then sectioned and again treated with acid; when this was done the internal material dissolved.

The unpressed, replaced graptolites belong to the genus *Climacograptus* and possibly *Climacograptus putillus* Hall. Text-figure 1 is a camera lucida drawing of one of the specimens, text-figures 2 and 3 are camera lucida drawings of thin sections. Text-figure 2 shows around to elliptical inclusions, some dark brown in color, others clear. Text-figure 3 shows a number of small pyrite crystals.

SYSTEMATIC DESCRIPTION

CLIMACOGRAPTUS Hall, 1865

"Simple biserial rhabdosome, bilaterally symmetrical; thecae parallel, their outer margin straight and parallel to rhabdosome axis, tubular, aperture within well defined excavation." (Hall, 1865, p. 71.)

CLIMACOGRAPTUS PUTILLUS Hall

Text-figs. 1–3

"Rhabdosome very small (9 mm. or less long) and narrow (1 to 1.3 mm. wide), elliptical

in section, widening gradually, and possessing a gently wavy median furrow on each lateral face; thecae tubular, little inclined to axis or rhabdosome in proximal half and subparallel to it in distal free half, closely arranged thecae (12 to 14 in 10 mm.); apertures straight and perpendicular to longer axies of thecae; nemacaulus thin." (Hall, 1865, p. 73.)

PREVIOUS WORK DONE ON THE CASTLEWOOD EXPOSURE

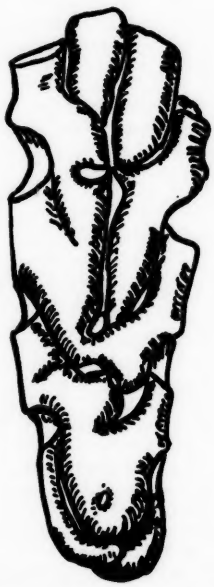
J. E. Keenan (1951) described the ostracodes from the Maquoketa of the Castlewood area. He concluded that the ostracode assemblage was as close to the Eden, Maysville and Richmond groups of the Ohio Valley as it is to the Maquoketa ostracodes described by R. C. Spivey (1939) from Iowa. He describes the Castlewood section (p. 561) as follows:

"Here the shale rests on the Kimmswick limestone and is overlain by a wedge of Grassy Creek shale or by Bushberg sandstone. The Maquoketa is about 18 feet thick, dark gray in color, and has from one to three thin phosphatic conglomerate zones near the top. Most of the ostracodes described here were taken from these zones. One of the zones, three inches thick and three feet below the top of the shale at the west end of the exposure, is much pyritized and contributed most of the best preserved specimens."

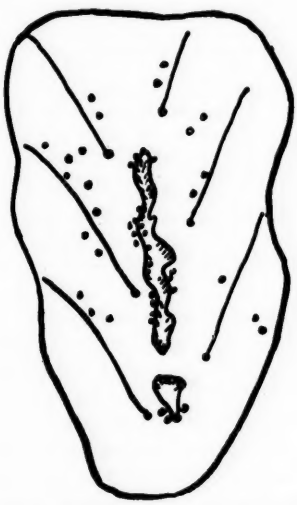
Branson (1938, 1944) published photographs of the Castlewood outcrop; but inadvertently labeled the Maquoketa, Grassy Creek. In 1947, Mehl & Thomas corrected this error (p. 4):

"The following section at Castlewood is the same as that figured by Branson. In Branson's photographic reproduction of the above section the Maquoketa was inadvertently labeled Grassy Creek. A thickness of only about three feet immediately beneath the unit labeled Bushberg belongs to the Grassy Creek and this is reduced to not many feet beyond the limits of the photograph. The part labeled Bushberg in

TEXT-FIG. 2—Thin section of *Climacograptus;* shaded circles brown inclusion, clear circles clear mineral inclusions. Length 1.8 mm.; width 1 mm.



TEXT-FIG. 1—*Climacograptus*, length 2.7 mm., width at widest part, 1 mm.



TEXT-FIG. 3—Thin section showing pyrite crystals scattered throughout. Length 2.5 mm.; width 1.3 mm.

the photograph is unit 4 and 5 of the above section, and the part labeled Fern Glen (F.G.) corresponds approximately to unit 10."

In 1939, H. N. Johnson (p. 94) discussed the Castlewood exposure and states:

"The Maquoketa at this locality presents quite a problem because of its unusual nature. At least the upper part of the shale has been reworked as is clearly indicated by the presence at the top of a black pebble conglomerate." [and on p. 134] "At Castlewood the top of the Maquoketa is marked by a thin conglomeratic zone, numerous dark pebbles averaging one centimeter in diameter and dark brown Maquoketa fossils are contained in a matrix of very hard, yellowish-brown, sandy shale which is also pyritic. The fossils are chiefly *Clidophorus neglectus* and *Orthoceras sociale*. The thickness of this zone is less than two inches. Immediately above is the Chattanooga shale."

The Kansas Geological Society Guide Book (8) records the locality as follows, p. 47–48: Stop 23:

"In this bluff are beds from the Kimmswick limestone to the Burlington-Keokuk. At this point mile post −2200 only the top 6 or 7 feet of Kimmswick limestone is exposed. Lying on the Kimmswick is approximately 20′ of gray-green Maquoketa shale of Upper Ordovician age. At this stop the Grassy Creek shales of Devonian age lie in contact with the Maquoketa shale. Microfossils are a great help in separating these two shales where they are in contact. Approximately 4 feet below the top of this shale section is a sandy conglomeratic zone, the pebbles being mainly phosphatic. At this locality Ordovician conodonts, graptolites and ostracodes have been found in the lower two thirds of the shale and Devonian fishes and conodonts in the upper third of the section. Overlying the Grassy Creek shale is approximately 17 feet of Bushberg. At the base of the Bushberg is a sandy conglomerate which contains great quantities of fish teeth (*Ptyctodus calceolus*). Above the Bushberg is approximately 60 feet of Chouteau limestone, the lower part containing 10–15 feet of interbedded red and gray-green shales and shaley limestones which constitute the Fern Glen member."

Although we have visited the locality several times—to date we have not been able to locate the Grassy Creek shale mentioned in the guidebook and originally recorded by Branson and recorded as Chattanooga by Johnson. The uppermost conglomerate is in direct contact with the Bushberg sandstone and the shales immediately below the conglomerate contain fragments of *Diplograptus* and thin shelled *Lingulas*. The basal Bushberg conglomerate has incorporated in it both Maquoketa fossils and Bushberg fossils. Many fragments of fish teeth were found.

In our collections we have two other samples of Maquoketa shale from different localities; the unpressed, replaced graptolite is found in both samples. The localities are: (1) 20 miles southwest of St. Louis on highway 21, ½ mile north of Rock Creek, and (2) Seales Mound, Jo Daviess County, Illinois, a small town 10 miles northeast of Galena, Illinois, or approximately 20 miles east, slightly south, of Dubuque, Iowa.

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AGE OF THE BAINBRIDGE LIMESTONE

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In a recent paper O. H. Walliser (1957, p. 30–31) describes highest Wenlock and Ludlow age conodonts from the Rhenish Schiefergebirge, the Frankenwald, and the Carnic Alps. Walliser (op. cit.) finds that the conodonts in these three areas are similar to those of the Aymestry limestone of the Welsh Borderland previously described by Rhodes (1953) and to Silurian material described by Branson & Mehl (1933) from the Bainbridge limestone of Missouri. The Bainbridge forms are cited as of Wenlock age by Walliser (op. cit.) and by Rhodes (op. cit.) following Branson & Mehl's (1933) citing the Bainbridge as of Niagaran age, the latter conclusion based on the earlier study of the megafossils by Flint & Ball (1926). Flint & Ball (op. cit.) correlated the Bainbridge with the Henryhouse and Brownsport formations of Oklahoma and Tennessee respectively on the basis of a similar megafossil fauna. It is commonly assumed by North American stratigraphers that the "Niagaran" is of "Middle Silurian," i.e., Wenlock age, but the faunal evidence for this correlation can now be shown to be partly in error as far as both the basal and upper portions of the "Niagaran" are concerned. The basal portion of the Niagaran, the Clinton group, contains fossils which are of upper Llandovery, i.e., late Early Silurian age as pointed out by O. T. Jones (1923) and agreed with by the writer. The upper part of the Niagaran is generally considered to include the Lockport and Guelph dolomites plus their equivalents. These dolomites, and their equivalents, of which the Bainbridge is one, are considered by the writer to be of lower Ludlow or highest Wenlock, i.e., early Late or latest Middle Silurian age because of the occurrence of Ludlovian and highest Wenlock eospiriferids of the *Eospirifer nobilis* type in those dolomites in Wisconsin, Illinois, and Indiana.

The Henryhouse, which contains a megafossil fauna similar to that of the Bainbridge, has been dated by means of graptolites as of Ludlow age (including the zones of *Monograptus nilssoni-scanicus* to *M. ultimus* = *M. leintwardinensis*) by Decker (1935, 1936). Brachiopods similar to those of the Brownsport and Henryhouse have been found by the writer in exposures described by Woodard (1951) from Spencer Mountain, Somerset County, Maine, where they occur together with ostracods including *Periphanaria* sp. cf. *P. muricata*, *Dizygopleura* sp. cf. *D. costata*, *Dibolbina* sp., and *Mirochilina* sp. (Berdan, 1956, oral comm.), which are of Late Silurian, i.e., Ludlow age.

Dr. Walliser (written comm., 1958) finds the conodonts *Polygnathoides emarginatus* (Branson & Mehl, 1933) and *P. siluricus* Branson & Mehl, 1933, common to both the Bainbridge and the lowest five meters of the Orthoceratenkalk of the Frankenwald (= zone 30 of Elles & Wood, i.e., highest Wenlock; see Greiling in Walliser, 1957, p. 28–29).

In view of the above, the writer concludes that the Bainbridge limestone is of early Ludlow or highest Wenlock age because its megafossils are similar to those of the Henryhouse (dated by means of graptolites

as Ludlovian by Decker, 1935 and 1936), its conodonts are similar to several units of Ludlovian and highest Wenlock age in western Europe (Walliser, op. cit.; Rhodes, op. cit.), and its brachiopods are similar to those of an un-named unit in northern Maine (dated as of Ludlow age by means of ostracods).

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JOURNAL OF PALEONTOLOGY, V. 32, NO. 5, P. 1031–1032, SEPTEMBER 1958

NOMENCLATURAL NOTES

KOZLOWSKIELLINA, NEW NAME FOR *KOZLOWSKIELLA* BOUCOT, 1957

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Dr. Valdar Jaanusson, Paleontological Institution, Uppsala has kindly drawn my attention to the fact that *Kozlowskiella* Boucot, 1957 (Senckenbergiana Lethaea, Bd. 38, pp. 318–323) is preoccupied by *Kozlowskiella* Přibyl, 1953 (The ostracodes of the Middle Devonian (Givetian) of Poland in the profile Grzegorzewice-Skaly in the Gory Swietokryskie; Sbornik Ustredniho Ustavu Geol., Svazek XX, pp. 233–344, Prague). I therefore propose *Kozlowskiellina* Boucot, 1957 (not *Kozlowskiella* Přibyl, 1953).

SUBGENERIC STATUS IN TAXONOMIC PALEONTOLOGY

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Recently Elias (1957, p. 377) commented: "Many paleontologists do not use the taxonomic category of subgenera, for soon after introduction, a subgenus is usually elevated to full generic rank." Apparently this situation has been derived from the somewhat obscure definition of the subgenus as given in the International Rules of Zoological Nomenclature, Article 6 (see Schenck & McMasters, 1956, p. 33), which states: "... From a nomenclatural standpoint they (genera and subgenera) are co-ordinate, that is, they are of the same value."

Whereas the present author is in no way in basic disagreement with the elevation of subgenera to generic rank (when the need for higher taxonomic status is apparent), it appears essential, if the use of subgenera in paleontological classification is to be of value, that, for convenience, a more rigid definition be proposed.

Gwyn Thomas (1956, p. 30) stated: "Subgenera could also advantageously be used more often as chronological divisions of evolving genera in order to express phylogenetic relationships." This appears to suggest a basic definition for the category, which may be formulated as follows: Subgenera represent the divisions of a genus, which in being infrageneric and subgeneric groups exhibit confined, single, or diverse, evolutionary-morphological characters of a type above that of the specific, but not of generic order, which, being a series, arise chronologically from the common ancestral (typical generic and subgeneric) stock dem, onstrating phylogenetic, or morphogenetic-development.

The use of the category in such a restricted sense has previously been demonstrated by individual workers (Elias, 1957, p. 378), recently it has been applied, in an artificial sense, to the classification of chronologically occuring, disjunct, holothuroid spicules exhibiting morphogenetic features (Hampton, 1958), and it appears probable that it will become of considerable value in micropaleontological studies.

The value of subgenera in taxonomic paleontology should not be disregarded, and the present writer supports the view of Elias (1957, p. 377), who wrote: "With the gradual advance of our knowledge of the evolution of various fossil organisms there arises a new need for the use of some well established generic names in a subgeneric sense."

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HERTLEINITES, NEW NAME FOR THE CRETACEOUS AMMONITE *HERTLEINIA*, PREOCCUPIED

RALPH W. IMLAY
U. S. Geological Survey

Leo G. Hertlein has called to my attention that *Hertleinia* Imlay 1957 (Washington Acad. Sci. Jour., v. 47, p. 275,276) is preoccupied by *Hertleinia* Marks 1949 (Jour. Paleontology, v. 23, p. 457). I propose, therefore, to substitute the name *Hertleinites* for *Hertleinia* Imlay. The type species remains *Neocraspedites aguila* Anderson (1938, Geol. Soc. America Spec. Pap. 16, p. 156, pl. 25, figs. 1–3, pl. 68, fig. 4) and becomes *Hertleinites aguila* (Anderson).

JOURNAL OF PALEONTOLOGY, V. 32, NO. 5, P. 1033–1034, SEPTEMBER 1958

NOTICES

FOSSILS IN THE PUBLIC DOMAIN

The editor regrets that the statement concerning fossils in the public domain (Jour. Paleontology, v. 32, p. 642–643, May 1958) was published without adequate explanation.

The article consisted of the draft of proposed rules and regulations to govern the collection of fossils on federal lands drawn up by a committee of the Society of Vertebrate Paleontology at the request of representatives of the U. S. Government after a conference in January 1957. The statement is submitted for suggestions and comments by interested members of the profession. Any questions concerning it or constructive suggestions should be submitted to Professor Bryan Patterson, Museum of Comparative Zoology, Harvard University, Cambridge 38, Massachusetts.

These are not rules now in effect and have not yet been submitted to the government agencies concerned for approval.

BRAZILIAN PALEONTOLOGICAL SOCIETY

Word has been received of the founding of the SOCIEDADE BRASILEIRA DE PALEONTOLOGIA on March 7, 1958 (Address: Av. Pasteur, 404, Praia Vermelha, Rio de Janeiro, Brasil). Forty-four Brazilian geologists are on the roster of Founding Members. The first President of the Society is Dr. Wilhelm Kegel, Vice-President, Dr. Carlos de Paula Couto, Secretary, Dr. J. R. de Andrade Ramos, and Treasurer, Dr. Rubens da Silva Santos. Dr. Kenneth E. Caster of the University of Cincinnati, Vice-President of the Paleontological Society, is on the roster of Founding Members of the new Brazilian Society.

The first Annual Congress of the new Brazilian Society of Paleontology will meet in September, 1958 in Belo Horizonte, Minas Gerais, with special attention to the famous caves of Lagôa Santa made famous over a century ago by the work of the Danish Paleontologist Peter Lund. The caves have yielded a rich Pleistocene mammalian fauna and intercalated indian burials which for long were supposed to be contemporaries of the mammalian remains.

In the near future, the new Brazilian Society will undertake the publication of a Journal of Brazilian Paleontology. Annual dues are set at 400 Cruzeiros.

ZOOLOGICAL NOMENCLATURE: NOTICE OF PROPOSED USE OF THE PLENARY POWERS IN CERTAIN CASES FOR THE AVOIDANCE OF CONFUSION AND THE VALIDATION OF CURRENT NOMENCLATORIAL PRACTICE (A.(N.S.)41)

Notice is hereby given that the possible use by the International Commission on Zoological Nomenclature of its Plenary Powers is involved in an application relating to the under-mentioned names included in Part 2 of Volume 16 of the *Bulletin of Zoological Nomenclature* which will be published on 6th June 1958.

(2) *Dactylioceras* Hyatt, 1867, designation of a type species for, in harmony with accustomed usage (Class Cephalopoda, Order Ammonoidea: Jurassic) (Z.N.(S.)956);

2. The present Notice is given in pursuance of the decisions taken on the recommendation of the International Commission on Zoological Nomenclature, by the Thirteenth International Congress of Zoology, Paris, July, 1948 (see *Bull. zool. Nomencl.* 4: 51–56, 57–59; *ibid.* 5: 5–13,131).

3. Any specialist who may desire to comment on the foregoing application is invited to do so in writing to the Secretary to the International Commission (Address: 28 Park Village East, Regent's Park, London N.W.1., England) as soon as possible. Every comment should be clearly marked with the Commission's File Number as given in the present Notice, and sent *in duplicate.*

4. If received in sufficient time before the commencement by the International Commission of voting on the application in question, comments received in response to the present Notice will be published in the *Bulletin of Zoological Nomenclature:* comments received too late to be so published will be brought to the attention of the International Commission at the time of the commencement of voting on the application in question.

5. Under the decision by the International Congress of Zoology specified in paragraph 2 above, the period within which comments on the applications covered by the present Notice are receivable is a period of six calendar months calculated from the date of publication of the relevant Part of the *Bulletin of Zoological Nomenclature*. The Part now in question will be published on 6th June 1958. In consequence any comments on the applications published in this part should reach the Secretariat of the International Commission at the latest by 6th December 1958.

FRANCIS HEMMING

Secretary to the International Commission on Zoological Nomenclature

JOURNAL OF PALEONTOLOGY, V. 32, NO. 5, P. 1035–1036, SEPTEMBER 1958

REVIEW

SOME FACTORS IN THE DISTRIBUTION OF FOSSIL CEPHALOPODS. R. A. Reyment. Stockholm Contributions in Geology I:6. Stockholm. 1958.

The subject of fossil cephalopod distribution has been taken up for thorough study in this paper, which deserves wide notice. This question has been touched upon casually in theoretical discussions on the matter by many previous authors but Dr. Reyment's paper yields additional important empirical data. These were obtained by experiments in various artificial and natural environments with plastic models of uncoiled and straight shells and intact and partly remodeled *Nautilus* shells. The author also contributes numerous notes on modes of occurrence and special shell anatomy of cephalopods based on his field and laboratory work in West Africa and Europe. Ecologic observations on modern cephalopods are considered.

A specific gravity of 2.63 for the shell material was used in the construction of the plastic models. This is the S.G. of living *Nautilus* shells and can be inferred to be approximately true for cephalopod shells in general.

The buoyancy of a chambered cephalopod shell was found to be dependent on the following main factors:

1. Shape of the shell and thickness of shell material
2. Form of the body chamber; this is considered the most important factor and determines essentially the mode of settling of a stranding buoyant shell
3. Number of septa and their shape
4. Dimensions of siphuncle
5. Effects of temperature, salinity and water pressure.

There are several general similarities but also differences in the mode of floating of empty endoceroid and orthoceroid shells. Neither will float if the body chamber exceeds the length of the chambered part by a certain amount (about one fourth in typical endoceroids, one half in typical orthoceroids). Otherwise both types float with the siphuncle beneath but the orthoceroid type is less stable in that respect. The larger the body chamber the more nearly vertical is the floating position (body chamber down); at maximal lengths of body chambers orthoceroid shells float vertically, whereas in endoceroid shells the angle of the length axis to the horizontal will not exceed 45 degrees. Both float in a horizontal position at certain intermediate ratios between body chambers and chambered parts and with the tip lower if the body chamber is very short.

Some curved and partly coiled shells may have sunk if the body chambers were large; for example, many scaphitoids and hamitoids. Turrilitoid shells may have been borderline cases. Baculitoid shells may have floated almost horizontally but the siphuncle was fragile and, hence, liable to mechanical destruction by water movement and pressure, so that water may have entered the shell and caused it to sink. Lituitoid shells floated at an angle to the vertical.

Coiled shells reveal great variation in buoyancy. The size of the body chamber is of principal importance. Remodeled *Nautilus* shells do not float if the body chamber occupies more than two thirds of the last whorl; many ammonites belong to this category. The relationship between volume of chambers and weight of the shell is also important: highly compressed and depressed shells are sinkers; quite a number of ammonites fall into this group. Very involute shells float more easily than evolute shells. Apertural structures (ears, lappets) decrease the buoyancy. Solid and thick types of ornament diminish buoyancy and hollow ornament increases uplift; the majority of ammonites studied in thin sections by the author have hollow sculptural elements with thickened crests.

The author discusses the difficulty in calculating the weight of ammonite shells and their buoyancy owing to complicated septal folding and unpredictable irregularities in the distances between septa; a further complication is the fact that septa are not invariably convex-outwards as conventionally considered. The distances between septa are of particular importance in the case of partial water filling owing to siphonal damage: filling of a large chamber may cause sink-

ing, whereas this may not happen if a small chamber becomes filled.

Attention is called to shell damage that may cause sinking. The author found that holes develop in *Nautilus* shells if they are left to float for long periods. This may be a result of bacterial activity at sites of imperfect secretion of calcium carbonate. Damage to siphuncles may be ascribable to wave action (close to the body chamber) and to the effect of water pressure at depth (damage occurring in inner whorls). The fragile ammonite siphuncles were readily ruptured by water action.

Fluctuations in temperature have a tendency to sink buoyant shells since the air expelled during rises in temperature is replaced by water when the temperature subsequently falls.

The author points out that cephalopod shells may be transported along internal surfaces of density discontinuities (primarily salinity). This may have been of importance in the dispersal of shells from the living habitat into various brackish environments which the animals could not have invaded in life. The author has carefully studied how shells floating in the surface layer are deposited. He has shown by experiments that coiled shells (floating in a regular position with body chamber beneath) can fasten in sticky lutitic sediments in shallow water; a photograph of a shell in such a position in Ordovician rocks supplies ample evidence that this happened in the past. Shells that drifted into very shallow water toppled over and stranded in the swash zone. It was found that they became buried in the course of a few hours by scooping sediment into the body chamber and "digging" themselves down under the influence of slight swirling movements caused by the swash. Shells could also be carried far inland and deposited together with terrestrial organisms (plants for instance), as described in previous literature.

Investigations into "paleodispersal" of organisms can be of great help in reconstructions of ancient environments. The investigation reported on above would seem to have certain potentialities in that respect. It is of great importance that it is based on some necessary premises: a worker taking on such a study should have expert knowledge of the group; he should consider its modern ecology and post mortem dispersal; he should carry out experiments in modern environments under controlled conditions.

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JOURNAL OF PALEONTOLOGY, V. 32, NO. 5, P. 1037, SEPTEMBER 1958

SOCIETY RECORDS AND ACTIVITIES

In accordance with Article 3, Chapter 1 of the By-Laws of the Paleontological Society, the Secretary submits the following nominations for membership in the Society. The list has been approved by the Council of the Society.

ARNOLD, ZACH MCLENDON, Museum of Paleontology, University of California, Berkeley 4, Calif.: J. Wyatt Durham, Robert M. Kleinpell, R. A. Stirton.

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